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Subject matter will focus on taxonomy and systematics, ecology, zoogeography, evolution, and behavior. Subdiscipline areas will include general invertebrate zoology, ichthyology, herpetology, ornithology, mammalogy, and paleontology. Papers will stress the results of original empirical field studies, but synthesizing reviews and papers of significant historical interest to southeastern zoology will be included.

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The Mammal Fauna of Carolina Bays, Pocosins, and Associated Communities in North Carolina: An Overview

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ABSTRACT.— This study represents the first attempt to inventory and evaluate the mammals associated with pocosins and Carolina bays. During a 4-year period, approximately 17,000 trap-nights and 200 field-days in 12 North Carolina habitat types produced specimens or signs of 40 species of mammals. Early, intermediate, and advanced seral stages of pocosin-associated plant communities varied considerably in faunal composition. Species regularly trapped or observed included *Blarina* sp., *Pipistrellus subflavus*, *Sylvilagus palustris*, *Sciurus carolinensis*, *Peromyscus gossypinus*, *Ochrotomys nuttalli*, *Urocyon cinereoargenteus*, *Procyon lotor*, and *Odocoileus virginianus*. Additional uncommon or geographically restricted, but apparently regular, associates were *Condylura cristata, Plecotus rafinesquii, Oryzomys palustris*, *Microtus pennsylvanicus*, *Synaptomys cooperi*, and *Ursus americanus*. Most mammal associates are ubiquitous species. Although total documented diversity is high, a large percentage of the fauna is either associated with edges of communities or of irregular occurrence. At least eight species and several additional subspecies reach the northern or southern limits of their ranges in pocosin-rich areas.

Fires, storms, and certain man-related disturbances, by creating a patchy mosaic of habitats, seem to exert positive influences on mammal density and diversity in pocosin communities. Since uninterrupted or unaltered successional development eventually leads to minimal habitat diversity, management of extensive pocosin areas is desirable if mammal diversity is to be maintained.

INTRODUCTION

Recent authors have commented on the almost complete lack of information on the vertebrates associated with Carolina bays, pocosins and successionally related southeastern Coastal Plain habitats (e.g. Wilbur 1981; Sharitz and Gibbons 1982). Although some mammal surveys have been conducted within or adjacent to pocosin habitats, published reports have addressed taxonomic status or geographic, not ecological, distribution, making it difficult to relate most existing information to specific plant communities. The most notable of these studies have been

various investigations of the Dismal Swamp fauna of northeastern North Carolina and southeastern Virginia (e.g. Merriam 1895a,b, 1896; Handley 1979). Rose (1981a) investigated mammals associated with "openings" in the Dismal Swamp. Sharitz and Gibbons (1982) presented some preliminary information on studies they are conducting in South Carolina bays, but only three mammal species—*Blarina brevicauda*, *Reithrodontomys humulis* and *Sigmodon hispidus*—were mentioned. Lee et al. (1982) provided preliminary mammal species lists for the various plant communities in North Carolina, including information on pocosins and Carolina bays. With these exceptions, information on the mammal fauna of these specific systems was previously unavailable. From 1980 to 1985 we surveyed the mammals of pocosins, Carolina bays, and their associated plant communities in the North Carolina Coastal Plain in order to obtain a better understanding of diversity and relative density of the mammal fauna.

Considering the widespread geographic distribution of pocosins and Carolina bays it is quite surprising that their vertebrate fauna is so poorly known. There are estimates of over 55,000 Carolina bays between southern Maryland and Florida (Sharitz and Gibbons 1982). Wells (1946) estimated pocosin habitats to have originally occupied over 20 percent of the Coastal Plain of North Carolina alone, and noted that there were over 300 square miles of pocosin in just three southeastern North Carolina counties. Since that time a good percentage of these areas have been drained, partially drained, and cleared for agricultural or silvicultural purposes, and some areas have been dammed to create mill ponds. Other areas have been protected from fire for so long that the plant communities have progressed beyond pocosin seral stages.

There is some uncertainty about the extent of loss of such habitats and the need for concern. Heath (1975) and Richardson (1981) provided general summaries of the decline of these wetlands, and most subsequent studies relied on these sources as the basis for major concern for pocosin habitats. Originally, Richardson (1981) stated that only 31 percent of North Carolina pocosins remained in a natural state, but Richardson (1983) acknowledged that his data sources were in error. McMullan (1984) suggested that the reasons for concern may be less serious than previously stated, owing to faulty data sources and incomplete or nonexistent inventories. McMullan (1984) also demonstrated, through an analysis of a 300-year historical land use study of the Albemarle-Pamlico peninsula of North Carolina, that pocosin communities have persisted in spite of a long history of clearing and draining, and many present-day pocosins have developed (or redeveloped) on abandoned farm lands. Assuming that the more recent reports are correct, it appears that the original estimates of habitat loss were too high.

Furthermore, because little information on the vertebrate fauna associated with pocosins is available, definitive statements made by previous authors concerning wildlife values of pocosins were premature. Currently, discussions about the unique biological value of pocosins and Carolina bays on the one hand, and consideration for their use in agribusiness, silviculture, peat mining, and waste disposal on the other, are commonplace, but in most cases detailed information on which to base management decisions is lacking.

Although the information presented here pertains only to North Carolina, we suspect that our findings could apply generally to other pocosins and Carolina bays in the southeast. However, we have little experience with these communities outside North Carolina. Our efforts to date have been focused on making species inventories of a large number of different communities throughout the North Carolina Coastal Plain. While we consider our results more than preliminary, problems associated with sampling the wide array of Carolina bays and pocosin communities make it impractical at this time to compare relative abundance and density of species in specific habitat types based on cumulative trap-night success. Additional studies are planned to develop more elaborate population profiles for specific pocosin plant communities.

HABITATS STUDIED

Pocosin habitats are defined with difficulty, since considerable confusion persists in the use of the term. It originated from the Algonquin Indian word "poquosin" and is one of the few Algonquin words adopted by European settlers. Tooker (1899) provided a detailed discussion of the origin, meaning and use of the term. In tracing its early use, by both Indians and early settlers, Tooker found that "pocosin" referred to a wide variety of low, wet areas extending from New England through the Carolinas. Among European settlers, the term was locally interchangeable with "dismals" and "galls" for describing swampy thickets.

Botanists and ecologists have likewise used the word to describe a variety of low, wooded, wetland habitats, and in many instances the terms bay, bayhead, shrub bog, or evergreen shrub bog have been used to describe pocosin vegetation types. The term "bay" is particularly confusing because it refers to a number of successional stages of Southeastern wetlands that support several species of bay trees (Sweet Bay, *Magnolia virginiana*; Red Bay, *Persea borbonia*; and Loblolly Bay, *Gordonia lasianthus*), while the term Carolina bay, partly named for the presence of bay trees, refers to elliptical depressions that often support pocosin vegetation. Carolina bays are permanent geological features and often are specifically named sites (e.g. Wolf Bay, Bladen County), while the

bay forests are successional stages of wetlands. Strict definition and delimitation are further hampered by the fact that many pocosins are situated within extensive palustrine systems and/or border estaurine systems. Such mixed areas often provide a rich mosaic of wetland habitats involving broad zones of transition and complex successional patterns. Extensive areas called pocosins are, in fact, often composed of swamp forest, hardwood forest, and marshes. There seems to be no precise botanical definition of pocosin, but the tongue-in-cheek description, "any low, wet area so thick you can't walk through it", captures well the nature of a pocosin.

Pocosins

Wells (1946) provided a general botanical analysis of pocosins in Holly Shelter, Pender County, North Carolina, and Kologiski (1977) investigated the vegetative communities of the Green Swamp, including several types of pocosin, savanna and related successional communities. Buell and Cain (1943) described the successional role and ecological requirements of Atlantic White Cedar, *Chamaecyparis thyoides*, forests in southeastern North Carolina. White cedar forests and savannas are both closely allied with pocosins. Additionally, Wells (1932), Woodwell (1956), and Sharitz and Gibbons (1983) provided overviews of pocosin vegetation, and Wells and Whitford (1976) presented a good outline of the successional development and fate of stream-head swamp forests, pocosins, and savanna communities.

Carolina Bays

Carolina bays vary in size from only a few to many hundreds of hectares, and an exposed sand rim of varying width normally occurs around a bay's perimeter. These depressions are naturally wetter at all seasons than are most surrounding areas, contrasting markedly with the dry sand rims, which support xeric plant communities. Most Carolina bays house pocosin communities in various seral stages, but some also contain sizable lakes, ponds, marshes, bogs, and swamps. In many bays, natural fire has been suppressed so long that the plant communities in them are now mature deciduous bay forests. The elliptical shape and the tendency for the deepest portion of the depression to be southeast of center often causes concentric vegetative zonation rings in the interior of the bays as well as an ecotonal ring around the perimeter. This type of vegetative zonation occasionally allows for considerable faunal diversity, even in small areas.

A vegetative profile of one Carolina bay near Jerome, Bladen County, was provided by Buell (1946a,b). We found, however, that by 1983 the area had been drained and lumbered so extensively that this bay no longer resembles Buell's description. This is unfortunate since it

was the only North Carolina bay where animal communities could have been related to a published vegetational analysis.

Unlike most other pocosin sites, Carolina bays are often located within xeric and mesophytic systems. Their islandlike nature often makes them more visually delineated and ecologically discrete. The wide spectrum of successional stages, combined with their close proximity to each other, makes them excellent study sites. In one of our principal study areas in Bladen County, bays are highly concentrated and successional stages probably achieve their greatest diversity.

Community Development and Structure

Various environmental factors dictate the type of pocosin community that develops on a particular site. The most conspicuous factors are surface and subsurface soil types, hydroperiod, and fire. The importance of the regularity and intensity of fire as it relates to season, hydroperiod, wind, and the accumulation of combustible vegetation cannot be overstated. Natural fires, and those started by Indians for game exploitation and later by Europeans for livestock range management, were all important for long-term maintenance of various seral stages of pocosins. Fire exclusion policies of the middle part of this century were detrimental to certain communities (particularly savannas), but recent understandings of the importance of regular controlled burning in certain Southeastern vegetation types for game and habitat enhancement and for wildfire control has, in part, alleviated this problem.

The characteristic and conspicuous plants of pocosins and Carolina bays are comparatively few. In most instances each species occurs in a majority of the vegetative community types and only its relative abundance or growth form changes. These variations in relative composition, however, may be dramatic, both visually and ecologically. The major plant associates (alphabetically by genus) are Red Maple, *Acer rubrum*; Wire Grass, *Aristida stricta*; Atlantic White Cedar, *Chamaecyparis thyoides*; Titi, *Cyrilla racemiflora*; Loblolly Bay, *Gordonia lasianthus*; Sweet Gallberry, *Ilex coriacea*; Inkberry, *Ilex glabra*; Fetterbush, *Lyonia lucida*; Sweet Bay, *Magnolia virginiana*; Black Gum, *Nyssa sylvatica*; Red Bay, *Persea borbonia*; Pond Pine, *Pinus serotina*; Bamboo, *Smilax laurifolia*; Pond Cypress, *Taxodium ascendens*; and Honey-cup, *Zenobia pulverulenta*. Species less uniformly distributed include Lamb-kill, *Kalmia carolina*; gooseberries, *Vaccinium* sp.; rushes, *Juncus* sp.; sedges, *Carex* sp.; Loblolly Pine, *Pinus taeda*; Longleaf Pine, *Pinus palustris*; and Cane, *Arundinaria gigantea*. These latter species are, however, often the dominant vegetation on certain sites.

Major pocosin community types include shrub bogs with scattered Pond Pine overstory, mixed conifer-hardwood shrub bogs, and pine-

shrub savannas. Early successional stages of all these types appear to be grass-sedge communities and later ones mature conifer-hardwood and evergreen bay forests. With long-term absence of fire, all eventually become deciduous bay forests. In these later stages cypress and Black Gum emerge on the sites with protracted hydroperiods, and Sweet Gum, *Liquidambar styraciflua*, and pines grow on drier ones. Thus, pocosins in general can be viewed as intermediate successional communities, often maintained in a subclimax stage by fire and hydroperiod, with the mature vegetational stages being suppressed for long periods on the wettest sites but developing relatively quickly on drier ones. Figure 1 depicts our perception of a general successional model of pocosin communities. Figure 2 shows various examples of the communities discussed.

Development of white cedar forests is unusual in that this species needs fire or other disturbance to remove vegetation so seedlings can develop. However, extremely hot fires destroy the peat soil and dormant seeds, and white cedar forests do not appear. Conversely, low intensity, fast moving fires do not destroy enough of the root stocks of competitive shrubs for cedar to become well established. When established, white cedar is extremely fire susceptible and persists only in the absence of fire. Young white cedar forests are usually pure, nearly even-age stands, and the density of such forests often inhibits the establishment of other tree species for about 40 years. After that time the trees begin to thin out and the nature of their crowns changes, which permits light to penetrate to the forest floor. At this stage bay forests develop rapidly, although individual white cedar trees may persist for long periods. The open savanna community requires a periodic disturbance by fire. If fire is suppressed for several consecutive years, many characteristic savanna plants vanish. (The above analysis is summarized from Wells 1946; Buell and Cain 1943; Kologiski 1977; Wells and Whitford 1976; and our personal observations.)

We have included the sand rims associated with Carolina bays and Coastal Plain stream-head forests in our discussion of animal distributions. In both sand rim and stream-head forest communities, fire plays an important role in maintaining community structure. The stream-head forest communities were considered by Wells and Whitford (1976) to be vegetatively similar to certain pocosin communities and we have also found them to be similar faunistically. Plant communities of the sand rims, while in direct contrast to pocosin vegetation types, are a characteristic vegetational feature of Carolina bays and are included in our discussion. These sand rims are dominated by Longleaf Pine; Turkey Oak, *Quercus laevis*; and Wire Grass.

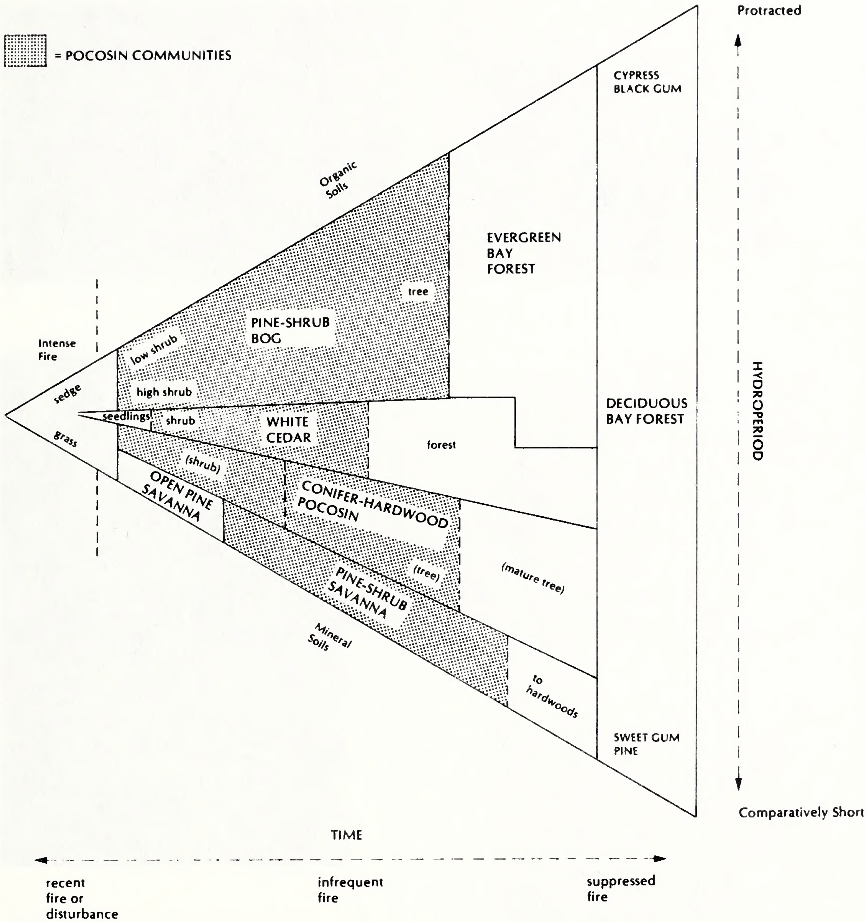
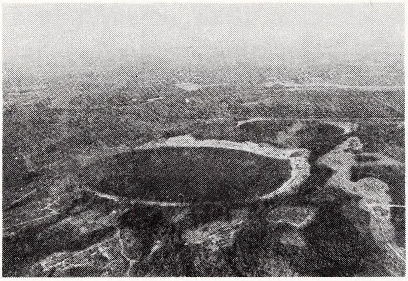


Fig. 1. Suggested pattern of vegetation development of pocosins and associated communities as related to disturbance, time, and hydroperiod (from Lee, in manuscript. Breeding bird communities in pocosins.)

METHODS

Almost 17,000 trap-nights were involved in this study. (Trap-nights equal the number of baited traps multiplied by the number of nights the traps are in place). Trap-night success is the percentage of catch per trap-night effort. Most trapping was done with Museum Specials baited with peanut butter, but Sherman live traps (2 sizes), Conibear, leg hold, Have-a-Hart type live traps, and mole traps were also used. Traps were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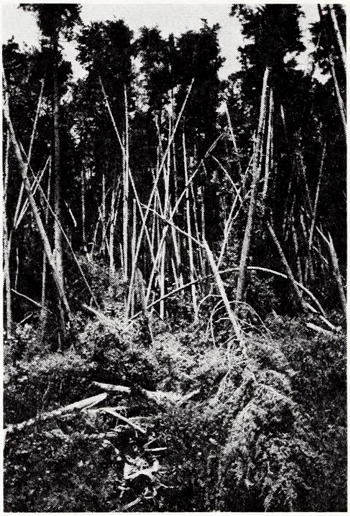


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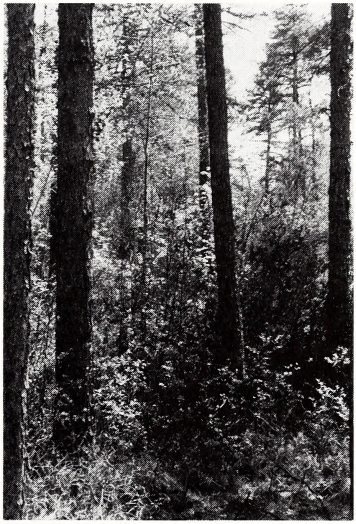

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Fig. 2. Habitats discussed in text. A. Aerial view of Carolina bays in Bladen County; note development of sand rim. B. Clay-based Carolina bay in Hoke County, vehicle parked on sand rim. C. White cedar forest in Green Swamp, Brunswick County; shrub bog in foreground. Note natural opening in mature forest, caused by storm damage. D. Pine-shrub bog, Bladen County. E. *Juncus* marsh developing in roadside ditch next to deciduous bay forest, Dare County. F. Pine-Wire Grass savanna, Carteret County. G. Longleaf Pine-Turkey Oak sand rim, Hoke County. H. Stream-head forest, Hoke County.

selectively placed within particular plant communities rather than distributed in grid patterns. Pitfall traps at two study sites, with and without drift fences, were left in place for extended periods and, although not included in our trap tallies, represent thousands of additional trap-nights. In addition, museum records, interviews with local residents, trappers and others familiar with the areas studied, personal sight records, and examinations of tracks and other sign, were used in compiling the faunal list presented here. Additional random information obtained from over 200 field-days and 25 evenings of mist netting and shooting bats is also included.

All North Carolina pocosins and Carolina bays that had been extensively studied and described in publications were visited to ensure that the community terminology used here was in general agreement with that of past studies. The difficulty of trapping small mammals in the Coastal Plain in general, of trapping in pocosins in particular, and unequal field effort in various community stages or areas, make it unlikely that our mammal lists for each plant community are definitive (bat information is particularly scarce). Because many of the areas studied are in transition from one community type to another, and many of our records are from ecotonal areas and disturbed or altered sites, assessing the species composition of specific communities is difficult.

The mammal fauna of Carolina bays, pocosins, and associated communities was studied in parts of Bladen, Brunswick, Carteret, Currituck, Dare, Hoke, Moore, Pasquotank, and Pender counties, North Carolina, between October 1979 and April 1984 (Fig. 3). Sites were not inventoried with equal field effort. The following sites were studied (total trap-nights per county are in parentheses): *Bladen Co.* (4,009)—Bay Tree Lake (Black Lake), Jones Lake, Little Singletary Lake, Salters Lake, Singletary Lake, Suggs Mill Pond (Horseshoe Lake), White Lake, one unnamed bay 3.2 km east of Kelly on NC 53, and another 17.8 km east of Kelly on NC 53. *Brunswick Co.* (266)—Green Swamp, 17.8 km north of Supply on NC 211; Sunny Point area. *Carteret Co.* (335)—Croatan National Forest, 4.8 km east of Newport. *Columbus Co.* (219)—Lake Waccamaw (town), Lake Waccamaw State Park. *Currituck Co.* (2,123)—Coinjock area and northward. *Dare Co.* (3,675)—mainland between US 64 and US 264. *Hoke Co.* (4,400+)—North Carolina Biological Survey Study Site at McCain. *Moore Co.* (200)—Weymouth Woods State Park. *Pasquotank Co.* (1,261)—Dismal Swamp, "Big Ditch." *Pender Co.* (0)—Holly Shelter Game Management area. The Currituck and Pasquotank counties data are from the eastern and southern edge of the Dismal Swamp, but include no true pocosin habitats. Nevertheless, the comparative geographic and abundance information obtained from these sites is informative. Specific specimen records

Fig. 3. Pocosin communities and Carolina bays in North Carolina (darkened areas; modified from Richardson 1981). Numbers correspond with study sites. *Dismal Swamp area*: (1) Currituck Co., Coinjock; (2) Pasquotank Co., "Big Ditch." *Pocosins and savannas*: (3) Dare Co. mainland, near East Lake; (4) Carteret Co., Croatan National Forest, 4.8 km east of Newport; (5) Pender Co., Holly Shelter Game Management Area; (6) Brunswick Co., Green Swamp, 17.8 km north of Supply. *Carolina bays and sand rims*: (7) Columbus Co., Lake Waccamaw; (8) Bladen Co., Bladen Lakes; (9) Hoke Co., N.C. Biological Survey Study Site, McCain. *Stream-head forest*: (9) Hoke Co., Biol. Survey Site, McCain; (10) Moore Co., Weymouth Woods State Park.

of only the more unusual species are cited in the following accounts. Plant names are from Radford et al. (1964).

RESULTS

Forty-one species of mammals were found in or adjacent to pocosins and Carolina bays. Fauna was composed of 1 species of marsupial, 5 insectivores, 8 bats, 2 rabbits, 15 rodents, 8 carnivores, and 2 hoofed mammals. Only 2 of these 41 species are exotics, and interestingly neither *Myocaster* nor *Rattus* was encountered. Two additional species, recently extirpated, are known to have been inhabitats of pocosin communities. Documented occurrence of extant species and trap success is

Table 1. Mammal species and their major habitat associations in the Coastal Plain of North Carolina. Habitat types are indicated at bottom of table; results from ecotonal communities are not included.

SPECIES	HABITAT TYPES												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Didelphis virginiana		x				x				x			x
Sorex longirostris	x						x	x	x	x			
Blarina sp.	x					x	x	x					x
Cryptotis parva		x								x			x
Scalopus aquaticus										x			x
Condylura cristata					x				x				
Lasionycteris noctivagans		x											
Pipistrellus subflavus				x									x
Eptesicus fuscus								x					x
Lasiurus borealis							x			x			x
L. seminolus										x			
L. cinereus		x								x			x
Nycticeius humeralis		x						x		x	x		x
Plecotus rafinesquii							x	x		x	x		x
Sylvilagus palustris	x			x					x				x
S. floridanus				x						x			x
Sciurus carolinensis					x	x	x	x	x				x
S. niger								x	x				
Glaucomys volans		x							x	x			x
Castor canadensis							x	x	x		x		x
Oryzomys palustris	x											x	x

	1	2	3	4	5	6	7	8	9	10	11	12	13
Reithrodontomys humulis	x											x	x
Peromyscus leucopus	x						x	x		x			x
P. gossypinus	x				x		x	x	x	x			x
Ochrotomys nuttalli				x	x		x	x	x				x
Sigmodon hispidus	x	x		x						x	x		x
Microtus pennsylvanicus	x												x
M. pinetorum										x			x
Ondatra zibethicus											x	x	x
Synaptomys cooperi	x												x
Mus musculus													x
Vulpes fulva										x			x
Urocyon cinereoargenteus							x	x	x				
Ursus americanus		x		x	x	x	x	x	x	x			x
Procyon lotor	x	x	x	x	x		x	x		x	x	x	x
Mustela frenata		x		x		x	x	x					x
M. vison							x	x			x		
Lutra canadensis											x	x	x
Lynx rufus				x	x			x		x			
Odocoileus virginianus	x	x	x	x	x	x	x	x	x	x	x		x
# days in field	12	9	10	26	20	5	27	21	13	33	ca 5	5	25
# trap-nights	812	335	0	1021	500	625	2758	502	635	1437	0	230	617
trap success (%)	10.3	2.08	-	1.55	1.41	0.56	2.01	6.74	5.45	3.80	-	3.91	9.72

Habitat types:
1. Grass/Sedge/Rush
2. Savanna
3. Pine Shrub Savanna
4. Pine Shrub Bog
5. Conifer Hardwood Shrub Bog
6. White Cedar Forest
7. Evergreen Bay Forest
8. Deciduous Bay Forest
9. Stream-head Forest
10. Sand Rim
11. Open Water/Lake Edge
12. Estuarine
13. Disturbed

Table 2. Mammal species associated with Carolina bays, pocosins and associated communities, arranged by county. Currituck and Pasquotank records are for Dismal Swamp habitats, but no true pocosin communities are represented. Counties are indicated at bottom of table.

	COUNTIES									
SPECIES	1	2	3	4	5	6	7	8	9	10
Didelphis virginiana	x		x	x	x	x	x	x	x	x
Sorex longirostris	x				x	x	x			
Blarina sp.	x				x	x	x	x	x	
Cryptotis parva			x		x		x			
Scalopus aquaticus	x				x		x	x	x	
Condylura cristata	x						x			
Lasionycteris noctivagans		x								
Pipistrellus subflavus	x	x		x			x			x
Eptesicus fuscus	x					x	x			x
Lasiurus borealis	x	x		x		x	x	x		x
L. seminolus							x			
L. cinereus	x	x						x		
Nycticeius humeralis	x	x				x	x		x	
Plecotus rafinesquii	x			x		x				x
Sylvilagus palustris	x				x	x	x	x		x
S. floridanus	x		x		x		x	x	x	x
Sciurus carolinensis	x			x	x	x	x	x		x
S. niger	x	x					x	x		x
Glaucomys volans	x						x			
Castor canadensis	x						x			
Oryzomys palustris	x	x			x	x			x	

	1	2	3	4	5	6	7	8	9	10
Reithrodontomys humulis	x				x	x	x		x	
Peromyscus leucopus	x				x	x	x			
P. gossypinus	x	x			x	x	x	x	x	
Ochrotomys nuttalli	x	x				x	x			
Sigmodon hispidus	x	x	x				x	x	x	
Microtus pennsylvanicus					x	x			x	
M. pinetorum	x						x			
Ondatra zibethicus	x				x	x			x	
Synaptomys cooperi									x	
Mus musculus					x	x	x	x	x	
Vulpes fulva	x					x	x			
Urocyon cinereoargenteus	x		x		x	x	x		x	x
Ursus americanus	x	x	x	x		x				x
Procyon lotor	x	x	x	x	x	x	x	x	x	x
Mustela frenata	x	x			x	x				
M. vison	x				x	x				
Lutra canadensis	x				x	x				
Lynx rufus	x		x			x	x			x
Odocoileus virginianus	x	x	x	x	x	x	x	x	x	x
# days in field	45	6	2	3	28	20	50	3	44	6
# trap-nights	4090	266	335	219	2623	3675	4400	200	1261	0

1. Bladen
2. Brunswick
3. Carteret
4. Columbus
5. Currituck
6. Dare
7. Hoke
8. Moore
9. Pasquotank
10. Pender

presented for 12 habitats in Table 1 and for the 10 Coastal Plain counties surveyed in Table 2. Typically, only 10 mammal species were encountered on a regular basis, and only 8 species were found in 50 percent or more of the habitats studied. However, 20 species were recorded in 50 percent or more of the counties surveyed, suggesting that habitat was far more locally restrictive to distribution than was geography. Disturbed habitats with early successional communities yielded the greatest diversity and density.

During this study only 366 mammal specimens were trapped in 9,472 trap-nights, but many additional animals were obtained by other means, and approximately 450 specimens were taken from borders of pocosin communities (7,000+ trap-nights). A composite trap yield success for all pocosin habitats sampled was 5.13 percent; trap success was generally higher for surrounding communities. Voucher specimens and series of the common species collected at each study site are deposited in the mammal collection of the North Carolina State Museum (NCSM).

SPECIES ACCOUNTS

Marsupialia: Opossums

Didelphis virginiana virginiana Kerr, Virginia Opossum. Although common throughout a wide range of Coastal Plain habitats and abundant in certain parts of Bladen County, the opossum is not usually associated with pocosins or Carolina bays and individuals were rarely observed in or around these habitats. Only one specimen was taken from the Dare County mainland and over a four-year period few road-killed individuals were seen there. This species is only slightly more common on the sand rims of bays.

Insectivora: Shrews and Moles

Sorex longirostris ssp., Southeastern Shrew. This shrew is uncommon but is found in a wide variety of habitats, including sand ridges adjacent to stream-head forests with dense ground cover of *Aristida*, shrubby ecotones of stream-head forests, *Juncus*-dominated clearings, and evergreen and deciduous bay forests. In Bladen, Dare and Hoke counties the subspecies represented is *Sorex l. longirostris* Bachman. Pagels et al. (1982) noted that their records for this race were evenly divided between open fields and young forests where ground cover is heavy. One specimen of *Sorex l. fisheri* Merriam (NCSM 2723) was collected by us in a swamp forest in Currituck County. Rose (1981a) collected individuals of *fisheri* in openings dominated by herbaceous vegetation in the Dismal Swamp. Both races are apparently absent from typical pocosin (shrub bog) communities.

Blarina sp., Short-tailed shrews. The systematics of *Blarina* in the

southeastern Coastal Plain of North Carolina is in need of study. Even though the area is within the range of *B. carolinensis*, specimens we have obtained from Carolina bays, principally in Bladen County, are of a large form closely approaching *B. brevicauda* in size and appearance. In upland areas of Bladen County, however, we found only *B. carolinensis*. French (1981) reported large specimens of *Blarina* from Sampson and Columbus counties and also remarked on the need for additional work on this genus in the North Carolina Coastal Plain. The large forms we collected were found in mature evergreen bay forests. *Blarina brevicauda telmalestes* occurs in pocosins and associated communities in northeastern North Carolina, and for many years it was known only from the Dismal Swamp region. Paul (1965), however, reported the subspecies in Hyde County, and we found it at several sites in Dare, Currituck, and Pasquotank counties. We have also found *B. b. telmalestes* as well as a large *Blarina* (presumably also *B. b. telmalestes*) in a wide range of successional communities in southeastern North Carolina, but most of our records are from wet forest floors.

Cryptotis parva parva (Say), Least Shrew. The Least Shrew is a common and characteristic species of Longleaf Pine-Turkey Oak-Wire Grass associations, sand rims of Carolina bays, Wire Grass savannas, and early successional communities with open canopies and dense ground cover. This shrew is not expected to occur in typical pocosin vegetative stages, although it frequently was collected in pitfall traps at several of the sand rim study areas.

Scalopus aquaticus howelli (Jackson), Eastern Mole. The Eastern Mole is characteristic of sand rims of Carolina bays, but is uncommon or absent from lower and wetter portions of Carolina bays, pocosins, and savanna habitats. Eastern Moles commonly invade partly drained, disturbed areas and may range into damper soils for short distances, but in wetter systems they are probably replaced by *Condylura*. The Eastern Mole was not found in the extensive palustrine system of Dare County.

Condylura cristata parva (Paradiso), Star-nosed Mole. The few Coastal Plain records for the Star-nosed Mole are probably an artifact of the difficulty encountered in trapping this species. Normally it is limited to damp areas around springs, creek bottoms, and bogs. Mole runs encountered in a stream-head forest in Hoke County and around the wet margins of Carolina bays in Bladen County were almost certainly made by this species. Hall (1981) listed *Condylura* from the Dismal Swamp in Virginia and from Garland near White Lake, a Carolina bay in Bladen County. We have additional records from the following Coastal Plain localities: *New Hanover Co.*, Carolina Beach (NCSM 3243); *Washington Co.*, Wenona (NCSM records); *Pitt Co.*, precise

locality not identified (NCSM records); *Robeson Co.*, Lumberton (NCSM records); and *Scotland Co.*, near Laurinburg (NCSM 3037). Most of these records, if not all, are associated with Carolina bays and mature bay forest communities.

Chiroptera: Bats

Lasionycteris noctivagans (LeConte), Silver-haired Bat. On the evening of 7 April 1984 we collected 2 (NCSM 4179-80) of 20 or 25 of these bats while they were foraging over a borrow pit pond in Brunswick County. The pond was in a savanna and the direction from which the bats emerged indicated that they were roosting either in the savanna, in a shrub-savanna-pocosin, or in both. The bats were foraging with *Lasiurus cinereus* and *Nycticeius humeralis*, and *Lasionycteris* became more abundant as darkness approached. Searching above the pond after dark with high intensity spotlights, however, revealed few bats. Silver-haired Bats are uncommon spring and fall migrants and winter residents on the North Carolina Coastal Plain (Lee et al. 1982). The normal period of occurrences for the species in eastern North Carolina is documented from 17 November to 3 May (100 years of records from NCSM files).

Pipistrellus subflavus (F. Cuvier), Eastern Pipistrelle. This small bat is common in low pine-shrub bogs but is expected in most of the other vegetation types discussed. Approximately 25 pipistrelles were seen feeding at treetop level in Holly Shelter, Pender County, on 25 July 1983; 2 of them (NCSM 4064-5) were collected. A single specimen (NCSM 4181) was collected of three found in 1983 in an abandoned house near Lake Waccamaw, Columbus County. Three specimens (NCSM 3535-6, 3725) were taken on various dates while they foraged over a pond in Hoke County. This site, dominated by Turkey Oak-Longleaf Pine habitat, is adjacent to a small Carolina bay and extensive stream-head forest.

Eptesicus fuscus fuscus (Palisot de Beauvois), Big Brown Bat. This bat is not particularly common on the outer Coastal Plain of North Carolina. A single specimen (NCSM 3888) was taken and one other observed, in an opening in a deciduous bay forest at Buffalo City, Dare County, on 27 April 1983. Another specimen (NCSM 3846) was collected on 6 July 1982 at McCain. Additionally, we saw a bat that appeared to be this species foraging adjacent to and over a pine-shrub bog in Pender County. In Bladen County, the Big Brown Bat was occasionally found associated with *Plecotus rafinesquii* in abandoned buildings.

Lasiurus borealis borealis (Muller), Red Bat. Red Bats were regularly seen feeding at subcanopy height above roads and other openings in all

mature forest types, as well as over water, in all study areas. Single specimens were collected from the sand rim at Singletary Lake and Salters Lake, Bladen County; the specimen from Salters Lake was collected while it was foraging on 20 February 1984. Records from Dare and Hoke counties indicate that this bat is also common above both xeric and palustrine communities, and we saw individuals feeding over study sites in Pender County. We have several times observed Red Bats migrating by day (April) through Pond Pine-shrub bogs.

Lasiurus seminolus (Rhoads), Seminole Bat. We have a specimen of this species (NCSM 3701) collected over the sand rim adjacent to a Carolina bay in Hoke County. Bill Adams, U.S. Army Corps of Engineers, has collected many of these bats over large bodies of water in southeastern North Carolina (NCSM). We therefore find it likely that Seminole Bats occur regularly over many bay lakes.

Lasiurus cinereus cinereus (Palisot de Beauvois), Hoary Bat. Migrants and winter residents of this species were seen and collected adjacent to savannas, pine-shrub bogs, bay forests, and similar areas. We think they were seeking cleared, open areas for foraging and were not found in pocosins *per se*. We have also observed the Hoary Bat over large rivers in the southeast and suspect that it regularly forages over bay lakes. The thick vegetation of white cedar and evergreen bay forests provides potential roost sites, but roosting in these habitats has not been confirmed. We saw a Hoary Bat flushed from a hollow stump during a controlled winter burn of a stream-head forest and sand ridge at Weymouth Woods State Park, Moore County, and several were seen in the spring of 1984 foraging over a borrow pit pond in a Brunswick County savanna. Our documentation indicates that dates of occurrence range from 28 September to 17 April.

Nycticeius humeralis humeralis (Rafinesque), Evening Bat. The Evening Bat was commonly seen flying at canopy height in savannas, and along the edges of mature bay forests and swamps adjacent to fields. We were told of a local pest exterminator who gassed and removed "bucketfulls" of these bats from a boathouse on White Lake, Bladen County. In July 1983 we collected one specimen of many seen flying over a savanna in Brunswick County. The stomach of this bat, collected during late dusk, was already filled with fragments of recently consumed insects.

Plecotus rafinesquii macrotis (LeConte), Rafinesque's Big-eared Bat. We have numerous records of this rare bat from the Bladen Lakes area, Bladen County, although only four of them were directly associated with bays. One individual was reported by a local property owner in a hollow Black Gum cut from the edge of White Lake, another was seen

by us in an abandoned hotel on this lake, one (NCSM 4018) was from an abandoned building at Lake Waccamaw, and another was found on a building at Singletary Lake State Park (NCSM records). The Dismal Swamp, where Handley (1959) reported *Plecotus* collected from hollow cypress trees in Lake Drummond, is the northernmost locality for this species on the Atlantic Coastal Plain. We have a specimen (NCSM 3938) from the southeastern edge of the Dismal Swamp, Gates County, and recent records from Dare County. Unpublished studies by Lee and Clark show that on the Coastal Plain this bat is restricted to river swamps and bay lakes bordered by mature swamp forests.

Lagomorpha: Rabbits

Sylvilagus palustris palustris (Bachman), Marsh Rabbit. The Marsh Rabbit is common in nearly all stages of pocosins, although it is most abundant in ecotonal areas adjacent to clearings, roads, canals, and lake edges. At Bay Tree Lake, Bladen County, we found it to be sympatric with *Sylvilagus floridanus* in a low Pond Pine-shrub pocosin adjacent to the lake. Bill Adams (pers. comm.) reported this same situation in a pocosin in Brunswick County.

Sylvilagus floridanus (Allen), Eastern Cottontail. This rabbit is characteristic of but not common on sand rims, and is rare to absent in most pocosin and Carolina bay areas. We did not encounter a single rabbit of this species on the Dare County mainland except around residential areas. So many other races of this rabbit have been stocked in eastern North Carolina that subspecific recognition of the original native form, *Sylvilagus f. mallurus*, probably has little meaning.

Rodentia: Rodents

Sciurus carolinensis carolinensis (Gmelin), Gray Squirrel. The Gray Squirrel is common in many stream-head forests, pocosins with mature trees, and bay and swamp forests. It is particularly common in areas dominated by mature Pond Pine where it forages extensively on cones. It is recorded from most mature habitats, both natural and disturbed, and is occasionally seen crossing sand rims, but is apparently absent from savannas. In Dare County we found extensive Gray Squirrel use of habitats containing mature Pond Pine. These trees retain their seeds for long periods, and fire is a major triggering mechanism for seed release. Thus, mature cones are available throughout the year and represent a major, and perhaps in some areas exclusive, food source.

Sciurus niger niger (Linnaeus), Fox Squirrel. This species is not usually regarded as a pocosin associate. The sand rims of Carolina bays, however, provide the open, fire-maintained pine forests that Fox Squirrels prefer and here they are often common. They do forage in stream-

head forests, and we have seen them regularly taking cover and foraging along the edges of pocosins. Although savannas would appear to provide ideal habitat for this squirrel, it occurs in them only when the savannas are adjacent to upland areas with oaks that provide the mast on which the squirrel depends. Most savanna records are from the fall.

Glaucomys volans volans (Linnaeus), Southern Flying Squirrel. The Southern Flying Squirrel is probably present at most sites inhabited by Gray or Fox squirrels, but we have no records from pocosins. A nest with young was discovered in the 100-foot fire tower at Jones Lake, Bladen County, in 1983, and the species is abundant on sand rims at the Hoke County study site where we regularly found *Glaucomys* in hollow trees and bird nest-boxes in ecotonal areas of stream-head bay forests and a Carolina bay. It is present but apparently not common in savannas, and often is found in cavities made by the Red-cockaded Woodpecker, *Picoides borealis*.

Castor canadensis Kuhl, Beaver. The Beaver was extirpated from North Carolina in the early 1900s, but was later restocked and is making a successful comeback. *Castor* is not a conspicuous or important part of the mammal fauna of pocosins and Carolina bays at this time. Active colonies exist on the Hoke County study area at McCain, in close proximity to Jerome Bog and Suggs Mill Pond, Bladen County, and along the southwestern edge of the Dismal Swamp. Flooding and removal of many larger trees by beavers maintain boggy areas in which many of the characteristic pocosin shrubs thrive. Both the southeastern *Castor c. carolinensis* (from Alabama), the subspecies native to North Carolina, and the northern form, *canadensis*, have been stocked on North Carolina's Coastal Plain.

Oryzomys palustris palustris (Harlan), Rice Rat. The Rice Rat prefers marshes and other open, wet areas abundant with grasses, rushes, and sedges, but such habitats do not usually occur in those pocosins or Carolina bays with intermediate or advanced successional development. One specimen of *Oryzomys* was trapped in a clearing at Little Singletary Lake, a Carolina bay in Bladen County, and another was taken in an evergreen bay forest in Dare County. Fire and man-made disturbances create or maintain early successional stages, and in such habitats the Rice Rat is often abundant.

Reithrodontomys humulis humulis (Audubon and Bachman), Eastern Harvest Mouse. Typically associated with early successional stages of pocosin communities, this mouse appeared to be equally common on both wet and dry soils, and was also present on higher ground adjacent to estuarine systems. Harvest mice were most common in unnatural dis-

turbed areas, trash piles, mowed road shoulders, and agricultural areas. We have no records from wooded habitats, although the species is found on the sand rims of Carolina bays and probably occurs in open savannas.

Peromyscus leucopus leucopus (Rafinesque), White-footed Mouse. On sand rim areas in Hoke and Bladen counties this mouse replaces *Peromyscus gossypinus*, but it is present in extremely low densities and trapped regularly only around trash piles and other places with ample cover. The species was more widespread in Dare County. In recently disturbed areas, it occurred sympatrically with *P. gossypinus* but was seldom as common. We found *P. leucopus* in drained mature deciduous bay forests with good ground cover off US 64 in Dare County, but failed to find *P. gossypinus* there. This was the only "natural" site where we collected *leucopus* in any vegetation stage remotely related to pocosin habitats.

Peromyscus gossypinus gossypinus (LeConte), Cotton Mouse. The Cotton Mouse was the most common species collected during our study. All pocosins, Carolina bays, stream-head forests, and swamps with woody vegetation, and most disturbed sites, were inhabited by these mice. We also collected specimens from clear cut pine-shrub pocosins.

Ochrotomys nuttalli aureolus (Audubon and Bachman), Golden Mouse. *Ochrotomys* was common in mature forests in all areas studied, and occurred sympatrically with *Peromyscus gossypinus*. We found the Golden Mouse to be common in flooded Pond Pine-cane pocosins in Dare County, and in evergreen bay and stream-head forests. It was most common in ecotonal areas where light permitted vines (particularly *Smilax*) to flourish, and absent from savannas, sand rims, and unforested habitats.

Sigmodon hispidus komareki (Gardner), Cotton Rat. The Cotton Rat was most commonly associated with dry, early successional stages, Wire Grass savannas, and various disturbed communities, and was uncommon on sand rims dominated by Wire Grass. At Bay Tree Lake we found a few *Sigmodon* in the detritus line along the eastern shore of the lake. Interestingly, these rats were not at all common on the Dare County mainland, and those that we did find were not in natural communities. At one Dare County site, where the plant community in a roadside swale matured from *Juncus* to grasses and shrubs over a 2-year period, *Sigmodon* replaced *Microtus*. The Cotton Rat apparently is absent from the Dismal Swamp (Handley 1979), although we have records from the southern and western edges of the swamp.

Microtus pennsylvanicus nigrans (Rhoads), Meadow Vole. The Meadow Vole was abundant in wet, early successional communities on the Albemarle-Pamlico peninsula. We found it wherever *Juncus* was dominant, and in *Spartina* marshes and road shoulders bordering pocosins. Dark individuals, which appeared to be *Microtus p. nigrans*, were collected as far west as Gates County, along the western edge of the Dismal Swamp, and on the Dare County mainland. Except for a few barrier island and salt marsh populations of *Microtus p. pennsylvanicus*, the Meadow Vole does not occur on the Coastal Plain south of Pamlico River. Consequently, it was not caught in any of our study sites in southeastern North Carolina.

Microtus pinetorum pinetorum (LeConte), Pine Vole. We found *M. pinetorum* to be rare, but collected it in the ecotonal area between Carolina bays and their adjacent sand rims in Hoke (NCSM 3830) and Bladen (NCSM 4182) counties, and in dry areas adjacent to streamhead forest. Most of the study sites we visited were too damp to support this vole, but it is common in some drained agricultural areas that apparently had once been Carolina bays.

Ondatra zibethicus macrodon (Merriam), Muskrat. Although found throughout most of the Coastal Plain in marshes, ponds, and shallow areas of lakes and impoundments, Muskrats are not generally associated with pocosins or Carolina bays. Only in the drainage canals within pocosin areas in Dare and Pasquotank counties were they common. We have reports of muskrats in Sugg's Mill Pond, Bladen County, but in this particular Carolina bay the water levels are artificially maintained by earthen dikes and dams.

Synaptomys cooperi helaletes (Merriam), Southern Bog Lemming. This disjunct Dismal Swamp race of the Bog Lemming had not been found between 1896 and 1979 and there was some concern that it was extinct. Subsequently it was collected by Rose (1981b) in both the Virginia and North Carolina portions of the Swamp. In addition, we have a single specimen (NCSM 4019; Lee et al. 1982) from near Elizabeth City, and David Webster, UNC-Wilmington, informed us that he has collected this lemming in a young upland pine plantation near Merchant's Mill Pond, Gates County, North Carolina. Thus, the race is considerably more widely distributed than previously known. Rose (1981a) documented its ability to invade clearings with heavy herbaceous ground cover. Intensive trapping on the Albemarle-Pamlico peninsula by NCSM personnel, in what we regarded as optimum habitat for the species, indicated that this rodent does not occur south of Albemarle Sound. In fact, it appears to occupy a pocket in northeastern North Carolina and southeastern Virginia in which *Sigmodon* is absent. Based

on recent habitat information it seems that these two rodents are ecologically similar in the Southeast.

Mus musculus (Linnaeus), House Mouse. This is the only exotic species that we encountered regularly in our study. Although common along road shoulders and windrows in Dare County, and in suburban sites in drained or altered bays in Bladen County, it was not found in any natural sites.

Carnivora: Carnivores

Vulpes fulva fulva (Desmarest), Red Fox. The Red Fox apparently avoids pocosins and is uncommon on sand rims. Agricultural workers in Dare County informed us that Red Foxes did not appear locally until extensive areas had been cleared for agriculture.

Urocyon cinereoargenteus cinereoargenteus (Schreber), Gray Fox. Unlike the Red Fox, *Urocyon* is common in most densely wooded habitats, including pocosins. Individuals are often seen running on sand rims and ridges between Carolina bays and stream-head forests.

Ursus americanus americanus (Pallas), Black Bear. With the exception of the Sandhills sites in Hoke and Moore counties, bear populations still persist in all of our study areas. In 200 field-days we saw five individuals, and fresh tracks were found on about a dozen occasions. Pocosin communities contribute to the diets of Black Bears. Buell and Cain (1943), for example, reported bears feeding on *Smilax* fruits, and on young *Smilax* vines growing from seeds in bear scats.

Radio telemetry tracking of bears has been conducted in Dare (Hardy 1974) and Bladen counties (Hamilton 1978; Landers et al. 1979). In Dare County bears appeared to use all cover types, including pocosins (Hardy 1974). The preferred habitats were characterized by the presence of diverse and generally dense vegetation and close proximity to relatively extensive roadless areas. Hardy (1974) listed the order of habitat preference as forested areas, older burns, more recent burns, and clearcuts. Landers et al. (1979) related seasonal habitat use in Bladen County to foraging, denning and escape behavior. Carolina bays, which comprise about 44 percent of the county, received the most use by foraging bears and contributed the greatest volume of natural foods to their diet. Corn was a major component of the diet in every month, and the principal food item during seven months of the year. All radio-monitored bears that denned were found to bed on nests on the ground in very dense thickets of Fetterbush and greenbrier. Large swamps provided the best escape cover, which is probably the most critical component of Black Bear habitat (Landers et al. 1979). Of 45 known bear mortalities

in Bladen County from 1974 to 1976 none occurred in swamp forests (Hamilton 1978). Most bays containing dense vegetation, though, were too small to provide adequate cover. Access roads on sand rims and between bays also increased the vulnerability of bears to hunters.

Procyon lotor lotor (Linnaeus), Raccoon. Raccoon tracks or foraging animals were seen or collected in all communities except white cedar forest, and at all sites studied. At no site were Raccoons particularly common.

Mustela frenata noveboracensis (Emmons), Long-tailed Weasel. Based on tracks, road-killed specimens, and interviews with trappers, weasels are regular but uncommon inhabitats of pocosin communities. We have reports from savannas (Brunswick County), bay and white cedar forested Carolina bays (Bladen County), and pine-shrub bogs (Dare and Bladen counties). This weasel is probably found in most woodland habitats.

Mustela vison mink (Peale and Palisot de Beauvois), Mink. We have only one personal record of this animal from the study areas, but Dare County fur trappers informed us that minks are rather common along local drainage canals. Specific sites described to us were in mature evergreen bay and swamp forests. We saw tracks in a dirt road bisecting a wet section of Jerome Bog on the Bladen-Cumberland County line.

Lutra canadensis lataxina (F. Cuvier), River Otter. This mustelid is relatively common in freshwater canals and estuarine systems bordering pocosins in Dare County, and we have accumulated enough records to assume it occurs in all the Bladen Lakes of Bladen County. Otters were not recorded elsewhere.

Lynx rufus floridanus (Rafinesque), Bobcat. Although we found Bobcats or their tracks in only a few habitats, they probably occur occasionally in most Coastal Plain habitats. Tracks were seen at nearly all our study areas, and their frequency indicated that Bobcats must be relatively common. Using radio telemetry, Lancia et al. (in press) followed eight Bobcats for one to five months in the Croatan National Forest, Carteret County. Home range was larger than reported in other studies in the Southeast and varied from 12.37 to 50.35 km^2, with males having larger ranges. Females avoided pocosins and preferred agricultural lands, but otherwise habitat use was in proportion to availability. Lancia (pers. comm.) noted that the animals they studied were associated with edges of pocosins when these habitats were used, and generally avoided interiors of extensive pocosins. A little-known book by the Hon. Wm. Elliott (1918) contains a chapter on hunting Bobcats in

South Carolina. Excerpts from part of this chapter (see Appendix to this paper) provide some anecdotal insights into the nature of pocosins as a refuge for game animals, the behavior of pursued Bobcats, and the perpetuation of eyewitness accounts of "black" panthers in the Southeast.

Artiodactyla: Hoofed Mammals

Odocoileus virginianus virginianus (Zimmerman), White-tailed Deer. White-tailed Deer were observed in all habitats and at all study sites. Deer are now widely distributed throughout the Coastal Plain, although from the turn of the century through the 1930s they were reduced to a few remnant herds confined to the pocosin areas of the Albemarle-Pamlico Peninsula and to the Green Swamp area. Restocking and protection have been successful and the adaptability of deer is seen in their presence in 12 of the 13 habitats presented in Table 1.

Capra hircus (Linnaeus), Domestic Goat. Feral goats are quite common in the low shrub pocosins in southern Dare County. Land owners queried by us were not aware of their origin or how long they have been present. Hill (1973) reported on some goats "gone wild" in the Dismal Swamp in Virginia. We have not included them in Tables 1 or 2.

Recently Extirpated Mammals

Canis sp., Wolf. Based on place names and bounty records of the early 1700's through the 1800's, there is no doubt that wolves ranged throughout eastern North Carolina. There is some question, in our minds, however, whether the wolves were *Canis lupus*, the Gray Wolf, or *Canis niger*, the Red Wolf, or both. The Red Wolf was found at least as far north as Charleston, South Carolina (records at the Charleston Museum), and there is no reason to suspect that it did not range into coastal North Carolina as well. Pocosins and Carolina bays would appear to make ideal haunts for Red Wolves. Elliot (1918) noted that wolves were almost extinct in the maritime sections of the Carolinas and Georgia in 1867. We are not aware of any bounties paid on wolves in the Coastal Plain of North Carolina after the mid-1700s. As indicated by records in the North Carolina State Archives, in 1721 Chowan County paid bounties on "bobcats, panthers and wolves this year."

Places named for wolves in eastern North Carolina include Wolf Bay, Bladen County; Wolf House Point, Currituck County; Wolf Pit Creek, Hoke County; Wolf Pit Township, Richmond County; Wolfscape Township, Duplin County; and Wolf Swamp, Onslow County.

Felis concolor ssp., Panther. We know of no Atlantic Coastal Plain specimen records that would indicate the subspecific status of *Felis con-*

color in North Carolina. It is reasonable to assume that *Felis c. coryi* (Bangs), like various other "Florida" races of mammals, ranged into the southeastern part of the state. Specific records for *Felis concolor* in the North Carolina Coastal Plain are few. We are aware of the following:

1721. Chowan Co. bounty records. (North Carolina State Archives).

1776. "Wicker Davis was paid by court 10 shillings for killing a panther." Carteret Co. court minutes, vol. X, page 327.

Some years before the Civil War. One killed in Rose Bay, Hyde County (NCSM records).

1900. Trapped in a pocosin in Craven County (NCSM records).

1930. Washington County, Lake Phelps, "skin seen by biologists" (NCSM records).

Additionally, there are at least five Coastal Plain localities named after Panthers, presumably each representing encounters of early settlers with this cat. There are three different Panther Creeks, one each in Duplin, Pitt, and Sampson counties; Panther Swamp, Northhampton County, and Panther Swamp Creek, Greene County.

Sight records of Panthers still continue to be reported. Lee (1977) surveyed the numerous reports, and the information in our files has led to the following conclusions: 1) no recent reports of panthers in North Carolina are authenticated by specimens, photographs, identifiable tracks, hair samples, or scats; 2) seemingly reliable reports accumulated over the last 80 years have clustered in a few specific areas; 3) the frequencies and localities of Panther reports are directly related to past and present distributions and numbers of White-tailed Deer; and 4) based on a four-point scale of reliability (Lee 1977), nearly all reliable Coastal Plain sight records are from pocosin-rich areas. Forty-four records of Panther sightings in 20 eastern North Carolina counties were reported to the State Museum in the 1970's, but none was substantiated by photographs, footprints, or by other means. Unless evidence to the contrary appears, we consider the Panther extirpated.

DISCUSSION

Of the 40 mammals found, probably only *Blarina* sp., *Pipistrellus subflavus*, *Sylvilagus palustris*, *Sciurus carolinensis*, *Peromyscus gossypinus*, *Ochrotomys nuttalli*, *Urocyon cinereoargenteus*, *Ursus americanus*, *Procyon lotor*, and *Odocoileus virginianus* occur with enough density or regularity to be considered typical (although not characteristic) inhabitants of pocosin/Carolina bay communities. When open savannas are included in this system, *Cryptotis parva* and *Sigmodon hispidus* should be included. All species, except possibly the Black Bear, can be found in equal or greater abundance in many other Coastal Plain habitats and therefore are not to be regarded as index species for pocosins.

In North Carolina, only a few species are so geographically restricted that they would not be expected wherever pocosin habitats exist. Two North Carolina mammals, *Microtus pennsylvanicus* and *Synaptomys cooperi*, are limited to the northeast section of the state. All others, except *Sciurus niger*, *Castor canadensis* and to a lesser extent *Ursus americanus*, appear to be more or less uniformly distributed throughout the Coastal Plain. The Fox Squirrel is absent from pocosin areas in the northeastern counties, probably because of a lack of adjacent sand rims, open canopy pine forests, and mast-producing oaks. Through restocking, the beaver is now widely, but not uniformly, established in the Coastal Plain. Bears have been locally extirpated from the Sandhills area.

Most of the mammals discussed here are opportunistic species that exploit early and intermediate successional stages of many types of plant communities. Several (*Sciurus niger*, *Glaucomys volans*, *Microtus pinetorum* and the aquatic mammals) are associated only with peripheral communities of bays (sand rims) or aquatic systems and not with pocosin vegetation *per se*. Most species appear to exist normally in low densities within true pocosins and become common only in disturbed areas or ones with temporary vegetative shifts caused by fire or storms.

Sequence of Succession

We interpret the sequence of successional changes of the plant/-mammal communities in the stages shown below (mammals listed in approximate order of abundance). It should be emphasized that these lists of characteristic mammals do not represent total faunal lists as presented in Table 1, but indicate only species regularly found in each major community type. The sand rim associates of Carolina bays, as well as those of other community types, are listed in Table 1.

Early Stages.— Sedge/grass/rush communities (canopy and shrubs removed by fire or man) and savannas.

Characteristic: *Oryzomys palustris*, *Sigmodon hispidus*, *Microtus pennsylvanicus, Cryptotis parva, Reithrodontomys humulis, Sylvilagus palustris.*

Occasional: *Peromyscus leucopus*, *Mus musculus*, *Blarina* sp.

Intermediate Stages.— Pine-shrub bogs.

Characteristic: *Peromyscus gossypinus*, *Pipistrellus subflavus*, *Sylvilagus palustris, Odocoileus virginianus, Ursus americanus.*

Occasional: *Sylvilagus floridanus.*

—White cedar forests (mature dense forest).

Characteristic: *Blarina brevicauda.*

Occasional: *Sciurus carolinensis.*

Advanced Stages.— Evergreen and deciduous bay forests.

Characteristic: *Sorex longirostris, Blarina* sp., *Sciurus carolinensis, Peromyscus gossypinus, Ochrotomys nuttalli, Urocyon cinereoargenteus, Ursus americanus, Procyon lotor.*

Occasional: *Sylvilagus palustris, Lynx rufus, Mustela vison, Plecotus rafinesquii, Didelphis virginiana.*

We have not adequately surveyed white cedar forests and savannas. Our limited information (Table 1), however, suggests low diversity and density in white cedar forests and variable or highly fluctuating densities in savannas. In the cedar forests, most mammal activity seems to be restricted to edges (we also found this to be true of breeding birds). In savannas, periodic flooding and fire limit populations, but the quick response of grasses and other herbaceous plants after burning provides excellent cover and food, and denuded areas are probably repopulated quickly.

Factors Affecting Density and Diversity

Natural ecotones, openings, and edges caused by land-use practices, were far more productive for mammal trapping and observing mammal signs than were the interiors of pocosins. This can be attributed to generally good cover in these areas, a richer diversity of food plants, and a slight relief in topography that provides temporary refuge from seasonal flooding. In grass and sedge stages we found high mammal densities, and in several instances had over 50 percent trapping success. Semi-flooded *Juncus* areas produced some interesting results. Early in our studies of one such site we found *Microtus* (60% of total catch), *Reithrodontomys* (23%), and *Oryzomys* (8%) to be the dominant mammals. In following years, however, as the community matured and grasses dominated the vegetation, *Oryzomys* (50%) and *Sigmodon* (33%) became the more abundant species. Artificially maintained systems (mowed, grazed and drained, etc.) created habitats in which species not typical of pocosins, such as *Scalopus*, *Sylvilagus floridanus*, *Mus*, and *Vulpes*, appeared and often became numerous.

Although small mammals of many types quickly colonize early (open canopy) successional stages (Rose 1981a, and this study), the limited plant diversity probably does not provide a year-round food base in the intermediate (i.e., pocosin) successional stages adequate to attract or support small mammals. Thus, except for ecotones and natural or man-made openings, typical pocosin communities support very low densities of mammals, and at any single site usually a low diversity of species as well (see above lists of early and intermediate successional species). In contrast, efforts were made to sample the interiors of pocosins and bays. The interior of these dense communities where the canopy

or subcanopy is closed do not seem to be frequented by any mammal species, although they are certainly used for refuge by several large species.

Overall, the influence of fire is more positive than negative for mammals. Plants associated with pocosins respond quickly to burning, and the new growth of herbaceous species and the temporary openings in shrub layers generally result in an increase in small mammals. Areas we trapped in mainland Dare County one and two years after a major fire in extensive Pond Pine-shrub and Pond Pine-cane pocosins produced higher trap yields than did adjacent unburned areas. Burned or clear-cut sand rims and burned stream-head forests also had higher trap yields than those that were unburned for long periods. The fire resistant pines, most shrub root stocks, and moist soils would protect arboreal and terrestrial species of mammals from burning.

In many areas the plant communities are perched on hard subsoils that form natural basins; these basins retain surface water in the organic topsoils. Root systems of many of the bay forest trees usually do not penetrate the subsoils, and the limited support offered by these shallow peat soils makes larger trees extremely vulnerable to strong winds and ice storms. In addition, frequency of blow downs is high because many such trees are "crown heavy," a result of early competition with the normally dense understory vegetation. During the spring of 1983 we found extensive uprooting and limb breakage of trees (particularly Red Maple, Red Bay and Atlantic White Cedar) in Carolina bays in Bladen County and white cedar forests in Brunswick County. This damage was caused by late March snow and ice storms. Hurricanes and tornados would certainly cause even greater damage. Buell and Cain (1943) observed areas where the weight of *Smilax* climbing into the canopies of white cedar forests caused trees to uproot. Thus, natural openings in advanced successional stages are commonplace. They provide numerous sites for shade intolerant plants and for early successional and ecotonal faunas to maintain populations during periods when pocosins are in intermediate and advanced stages of development. Modest mammal diversity and density is apparent in such openings.

Degree and duration of flooding of pocosin communities is extremely variable. In general, areas with organic soils have protracted hydroperiods, whereas those with mineral soils have comparatively short hydroperiods. Local topography, the nature of soil types of adjacent communities, and land drainage also affect the amount of standing water. As expected, the soils in most communities remained saturated for extended periods. However, presence or absence of small mammal populations is dictated by the retention of standing surface water. The following comments provide examples of the effects that flooding has

on the composition of local mammal diversity and density (as gauged by trap-night success, shown in parentheses).

Dare County.—North side of Milltail Lake; 525 trap-nights in a 40-70 year pure stand of white cedar yielded three *Blarina brevicauda* (0.56%). A dense ground cover of sphagnum and other mosses, and numerous stumps and fallen logs, provided ideal microhabitats for small mammals. However, a later visit to the site revealed that strong winds regularly pushed lake water deep into the cedar forest, leaving only small, isolated hummocks unflooded.

Bladen County.—Salters Lake. Regular winter flooding, and periodic partial flooding at other seasons, of a mature Carolina bay forest apparently limits the local fauna in the bay forest. In 1,120 trap-nights in winter we collected only 6 *Peromyscus gossypinus* and 1 *Ochrotomys nuttalli* (total 0.62%), but in April, after standing water subsided, trap success (1.39%) was somewhat higher. *Blarina* sp. were also present but collected only in pitfall traps.

Hoke County.—McCain study site. In trapping the interior of a 2 hectare Carolina bay dominated by high shrub, in which areas with good cover for small mammals were numerous, we collected one adult *Peromyscus gossypinus* in 460 trap-nights (0.2%). Although the interior of the bay remained free of long-term standing water for at least two years (1980-82), heavy rains for extended periods in the spring of 1983 flooded over 80% of the interior of this bay and the clay-based subsoils retained the water for at least four months. Deer and rabbit (presumably *S. palustris*) sign were the only indications that the interior was used by mammals other than *Peromyscus*. Density and diversity were greater around the edges of the bay.

Pender, Dare, and Bladen Counties (shrub bogs).—On all visits, standing water was so prevalent that we did not normally attempt to set traps. (One attempt at trapping in Dare County yielded no mammals in 250+ trap-nights.) Even in the long-term absence of flooding, mammal populations in the interiors of pocosins probably are depauperate, an effect of seasonally limited food supplies. The characteristic plants are not true mast producers, and the majority of plant species hold their seeds for extended periods, rendering them inaccessible to ground-foraging mammals. In the interior of dense, intermediate-to-advanced pocosins, the exclusion of light prohibits flowering and fruiting of most understory plants (pers. observ.). From midwinter through early spring (normally the typical flood period) food resources in pocosin interiors are minimal. In all seasons very low raptor densities correlate with low densities of small mammal prey, a further indication of minimal availability of food plants for rodents. Breidling et al. (1983) addressed the problems of interpreting low density and diversity in four Dismal Swamp

plant communities. Interestingly, they suggested that no single factor was responsible, but discussed the impacts of low food availability and flooding.

The paucity of small mammals in pocosins and related communities can be illustrated by comparing trap-night success in those habitats with success in other habitats. For example, 3,000 trap-nights in pocosin communities (data pooled from Bladen, Hoke and Dare counties) had only a 2.06 percent capture success, and 1,000 trap-nights in mature evergreen bay forest in Bladen County had 1.23 percent success. On the other hand, 2,000 trap-nights in non-pocosin habitats in Currituck County averaged 6.1 percent trapping success, and 365 trap-nights in upland habitats of various types adjacent to Carolina bays in Bladen County yielded 7.12 percent success. The point here is that plant communities, not geography, are responsible for the relative densities.

Pocosin Systems as Refugia

Lee et al. (1982) discussed the occurrence in pocosin-rich areas of relicts such as *Synaptomys cooperi*, semi-relicts such as *Condylura cristata* and *Blarina brevicauda*, and species at the limits of their ranges. About 25 percent of the mammals associated with pocosins fall into one or another of these categories. Species that reach their northern distributional limits on the Atlantic slope within the Dismal Swamp area include *Plecotus rafinesquii*, *Sylvilagus aquaticus*, *Peromyscus gossypinus*, *Ochrotomys nuttalli*, and to a lesser extent *Sigmodon hispidus*. Except for fragmented populations of *Condylura cristata* and saltmarsh populations of *Microtus pennsylvanicus* that occur farther south, the Dismal Swamp area is also the southern limit for northern species that invade the southeastern Coastal Plain on the Atlantic slope. These include *C. cristata*, *M. pennsylvanicus*, and *S. cooperi*, and possibly *M. lucifugus* and *B. brevicauda*. Furthermore, *Condylura cristata* and *Sorex longristris* each reach the southern extremes of their ranges in pocosin-like communities, the former in the Okefenokee Swamp, Georgia (Paradiso 1959) and the latter in the Green Swamp, Polk County, Florida (Hill 1945). Their southernmost populations appear to be somewhat disjunct from populations to the north.

Pocosin habitats may have provided refugia for both northern and southern species since Pleistocene times, allowing populations to persist beyond otherwise normal distribution limits. The protective evergreen vegetation and the heat retention of high water tables should buffer the extremes of severe winter weather, while shade and evaporative cooling could be expected to ameliorate extreme high temperatures of Coastal Plain summers. Hibbard (1960) postulated that in the late Pleistocene (ca. 16,000 years ago) a period of climatic equality existed, in which

milder winters and cooler summers prevailed. These conditions allowed northern species to extend farther south and subtropical species farther north than they do today. This hypothesis is supported by evidence from various Southeastern fossil deposits (Holman 1976, 1982; Slaughter 1975). It is well documented that boreal elements were established in the Southern Applachians during the Pleistocene, but the presence of northern species in the Coastal Plain is not generally recognized. Whitehead (1963) discussed northern elements of Pleistocene flora in the Southeast and included information on two North Carolina Coastal Plain bays. Based on fossil pollen from Singletary Lake and Rockhound Bay, Whitehead showed that northern plants once were present in eastern North Carolina.

Whether floral and faunal elements reached their distributional limits as a result of the effects of glacial displacements and interglacial warming periods as is widely accepted, or did so simultaneously during a period of climatic equality, is not critical to this discussion. Either situation could produce the current assemblage of northern and southern elements that persists on the outer Coastal Plain of North Carolina. However, it is interesting that in some areas, well beyond their typical distributional limits, both northern and southern elements now coexist. As the climate shifted to the present regime, some relict and semi-relict populations were stranded along the outer Coastal Plain as well as in the southern Appalachians. Just as frost pocket bogs, areas of high elevation, and cove forests provided local refugia in the mountains, pocosins and Carolina bays apparently have done so on the Coastal Plain.

Pocosins as Key Coastal Plain Habitats

In addition to their roles as geographic refugia and climatic buffers, pocosins and Carolina bays were important as natural stands of early successional habitat. Their subclimax communities and complex zonation provided habitats for early to intermediate successional mammals that in precolonial times would not otherwise occur regularly on the Coastal Plain. Today, pocosins and related communities are not critically important for the geographical maintenance of most early successional mammal species because grazing, mowing, lumbering and similar activities produce a wide array of early successional stages over extensive areas. For example, Robinson and Lee (1980) pointed out that *Marmota monax* was unable to invade the Piedmont Plateau and Coastal Plain in the Southeast prior to extensive artificial maintenance of early upland communities and corriders for dispersal. The same is probably true for *Vulpes fulva* (Lee et al. 1982). Thus, for animal species already associated with pocosins and therefore widely distributed across the Coastal Plain, local expansion of their populations into disturbed

upland habitats is not surprising. In other words, species that may have been confined to pocosins in the past because of ecological restrictions are now able to exploit a wide array of disturbed community types as a result of agricultural and other activities.

Since pocosins and Carolina bays are extensive on the outer Coastal Plain, dispersal of small lowland mammals from one to another is feasible. River floodplain swamps can also facilitate dispersals of pocosin colonizers. Although these swamps would provide climatic buffers similar to those found in pocosins and Carolina bays, their frequent and rapid flooding and periods of protracted submergence make them unsuited to support permanent small mammal populations. Compared to adjacent upland communities, our trapping experience indicates that Coastal Plain swamps have extremely depauperate mammal faunas.

Bears, deer, bobcats and, until recent times, probably panthers and wolves, frequented pocosins and Carolina bays in the Coastal Plain. Within the last century most of those species had become confined to these areas, but this may have been an artifact of uncontrolled harvest before modern game management programs were developed and not a reflection of the specific habitat needs of these animals. Populations simply persisted in the inaccessible reaches of extensive pocosins longer than they were able to in other parts of the Coastal Plain. In eastern North Carolina, White-tailed Deer became restricted to a few pocosin areas by the turn of the century, and only in the last 30 years or so have they again become common in other areas and habitats.

Preservation and Management

We are concerned about pocosin preservation, but find the argument that these areas harbor many rare and unique faunal elements to be overstated, at least for mammals and birds (personal observations). As we have shown, pocosin mammal faunas generally consist of species with wide ecological tolerances and abilities to exploit early successional stages and areas disrupted by human activities. Pocosin areas should be preserved for a variety of reasons, but our present knowledge of the vertebrate fauna leads us to suggest that wildlife values for mammals (except the Black Bear), may not be a primary concern. Our results indicate that some types of alterations, when followed by normal successional patterns, actually increase species diversity and density of mammals and birds in Carolina bays and pocosins. Unpublished results of research by others indicate that this may be true of a variety of vertebrates. This is not surprising, because many such alterations simply change pocosin habitats in ways similar to those in which they are modified by fire and fluctuating water tables.

Lee and Funderburg (1977) discussed the conservation status of

North Carolina mammals, and listed as "status undetermined" *Blarina brevicauda telmalestes*, *Sorex longirostris fisheri*, *Lasiurus seminolus*, *Plecotus rafinesquii macrotis*, *Microtus pennsylvanicus nigrans*, and *Synaptomys cooperi helaletes*, all associated with pocosins and Carolina bays. *Ursus americanus* was considered of special concern, and *Felis concolor* as endangered and possibly extirpated. Later information on the "undetermined" species and races has shown them to be more common or widespread than previously suspected (see Lee et al. 1982; Rose 1981a; and this study). The number of known localities of extant populations has at least doubled for all these mammals, and some are now known to be widespread and even common. In the case of the Black Bear, though, pocosins and related habitats play a more than minor role where survival is concerned. A significant percentage of the surviving Coastal Plain bears is closely associated with pocosins and Carolina bays. Modern hunting methods, however, may make even extensive pocosins unsafe sanctuaries for bears.

The classification of pocosins and Carolina bays as types of wetlands, although in our opinion correct, has led others to a general assumption of high wildlife values despite the lack of systematic inventories. Misconceptions, absence of standard definitions, and lack of comparative information from other Southeastern wetland habitats, have also contributed to the problems of inventory and projection of habitat loss. Accurate assessments of the wildlife values of pocosins are further hampered by the lack of comparable historical comparisons of the mammalian fauna in the Southeast in general, and in the North Carolina Coastal Plain in particular.

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Appendix

The Hon. Wm. Elliott and his friends regularly employed dogs to hunt Bobcats in Carolina bays and bay heads near Beaufort, South Carolina. The following is Elliott's (1918:142-145) description of the habitat and the hunt.

"...quagmire at the surface, briers above (wherever their places were not preoccupied by bay-trees, that, for want of elbow room, had grown up as straight as canes, and almost as close)... and where the cat... had ensconced himself behind an entrenchment of briers, which hounds, unless their blood was heated by pursuit, would not willingly enter—so that he remained undetected.

"The hounds had not long entered the thicket, in which (from finding at its edge the remains of a half-devoured rabbit) we concluded that the cat still lurked,... and soon, a burst from the pack assured us that the cat was roused... But he keeps the cover, which is so thick as to defy the keenest sight; and circles it securely, leaving the dogs to tear their way through the briers. 'Ha! what is that? a shot!—another!'... Another shot! ah, now they pause—one savage growl—one stifled cry—and all is hushed..." [Three hunters surrounded the bay and each shot one or more times at the cat.]

"'How now?' says the judge, 'what hocus pocus is here? This is a tawny, leopard-like animal, while I pronounce the cat I fired at to be bigger and blacker; I saw it clearly as it rolled over in the swamp at the flash of my gun.'

"'My opinion, in this case, is precisely the same,' said the doctor. 'I fired at a black cat; the dogs must have changed cats during the chase!'

"'So much the better, gentlemen,' said I; 'we shall then have two cats, instead of one. Put on the hounds, boys!' They were taken to the point from which the doctor fired; but the stupid animals could find no trail, but that which led them again to the spot on which the tawny cat lay dead!

"... the cat, being duly subjected to a post-mortem examination, was found to have been struck by four out of the six shots fired at him—and the doctor's shot, of peculiar size, being lodged in his body, left no doubt of the fact, that the black cat of the doctor and judge was no other than the tawny cat of the rest of the field. Whether the change of color was in the skin of the cat, or the eye of the sportsman, or the distribution of light, we leave philosophers to determine."

Sympotthastia Pagast (Diptera: Chironomidae), an Update Based on Larvae from North Carolina, *S. diastena* (Sublette) comb. n., and Other Nearctic Species

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ABSTRACT.— Chironomids from the Nearctic believed to belong to *Sympotthastia* Pagast have been verified. They have been described and keyed against the well-known Palaearctic species. Generic descriptions of the male imago and pupa are expanded to include these species. Species found in the Nearctic in the larval stage, *S. fulva* Johannsen, a species near *fulva*, and *S. zavreli* Pagast, are contrasted with a generic larval description. The nearctic *S. diastena* (Sublette) comb. n., known only in the adult stage, is redescribed using two imagos collected in Oregon.

INTRODUCTION

This paper offers a taxonomic and ecological summary of all known species of *Sympotthastia*, which should be identifiable using the generic descriptions and keys provided. Species are separable only by minor differences, but two species groups are discernable.

The Palaearctic *S. zavreli*-group consists of *S. zavreli* Pagast, *S. spinifera* Serra-Tosio, and *S. macrocera* Serra-Tosio. Most of these species are well described in all stages (Serra-Tosio 1971, Ferrarese and Rossaro 1981). An unassociated larva found in North Carolina is keyed and described herein as *zavreli* (cf. Thienemann 1952), and this is the only member of the *zavreli*-group to be found in the Nearctic.

The Nearctic *S. fulva*-group consists of *S. fulva* (Johannsen), *S. diastena* (Sublette), a species near *fulva*, known in the larval stage, and a pupa described by Saether (1969).

Sympotthastia fulva was described at all stages by Johannsen (1921, 1937) with an emended description of the adults by Sublette (1967). I believe that this species is properly placed because the imagoes of both sexes were described from associations with the immatures reviewed for this paper. Dr. Dean Hansen identified two slides of male imagoes as *S. diastena*. This is a new combination with which I concur;

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see its new description below. The holotype was poorly mounted and much smaller and less setiferous than these finds of Hansen, but the phallapodeme unmistakably belongs to *Sympotthastia*. Following the criteria of Serra-Tosio (1971), an attempt was made to diagram the male imagoes of *Sympotthastia* in their phylogenetic order (Fig. 14).

Terminology used in my keys and descriptions follows Saether (1980), but Saether did not illustrate a Diamesini. Several terms used for parts of the male hypopygium were seemingly interchangeable, namely superior volsella and aedeagus. I decided to use his term, superior volsella (SVo), to describe the anteromedial portion of the phallapodeme that is apodemal in nature, that is, this structure is heavily sclerotized and articulates with the sternapodeme. This is illustrated for the Protanypini (Saether 1980:Fig. 13), but I think this structure should be consistently present in some form or another in all Diamesinae. The putative aedeagus is only a flaring of the lower phallapodeme in the Orthocladiinae (Saether 1980:Fig. 16). Saether, however, changed his terminology to aedeagus sensu Hansen and Cook (1976) for most of the Diamesini. Aedeagus, or a penislike, intromittent structure, is present as a secondary, microsetigerous lobe of the phallapodeme in most of the species of the sister genera *Potthastia* and *Sympotthastia*. It seems proper to refer to this lobe of the phallapodeme as the median volsella (MVo). The Diamesini have an anteromedial, hirsute lobe, which may not be very well expressed, on the gonocoxite resembling that of Saether (1980:Fig. 16). This report uses Saether's term, inferior volsella (IVo) for this lobe such as it exists in *Sympotthastia* (see Fig. 12).

The following ratios are expressed in key as percentages:
Leg ratio = first tarsomere / tibia;
Palp to face = lengths of palpal segments 2-5 / facial width at eyes;
Venarum ratio = length of cubital vein (from the arculus to its fork) / length of medial vein.

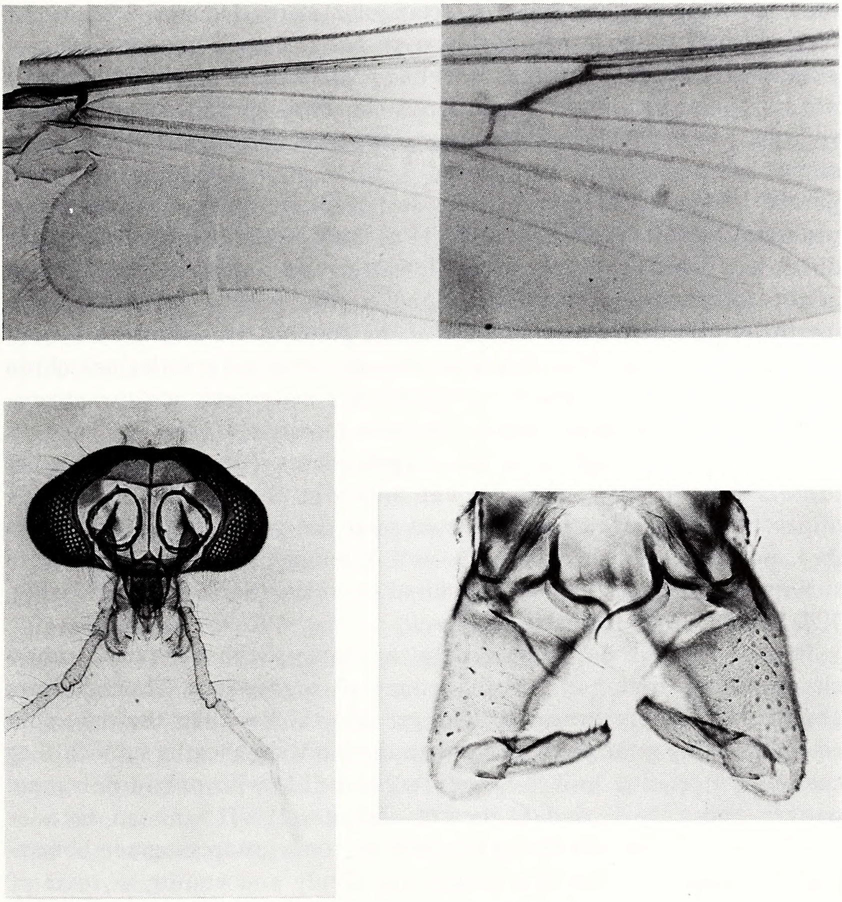
Sympotthastia Pagast

Sympotthastia Pagast, 1947:457, type species, *S. zavreli* Pagast, orig. design.; Serra-Tosio, 1968:129-130 and 1971:267-268 (descriptions of adults and pupae).

Diamesa heterodentata Botn. et C.-Cure(?), Pankratova, 1970 (incomplete larval description but spoonlike premandible possessing lateral teeth).

Nec Symp. sp. Simpson and Bode, 1980:30 (= *P. gaedii* Mg.).

Male.— Color uniform and dark. Wing 3-4 mm; body 3-6 mm. Eye naked between lenses (X400) and reniform. Antenna with 13 plumose flagellomeres; AR usually 2-3; A_{13} relatively long and slightly swollen apically below the subterminal spine. Postorbital setae biserial at mid-



Figs. 1-3. *Sympotthastia diastena* from Oregon: 1, wing; 2, head showing endoskeleton; 3, hypopygium showing endoskeleton.

eye; outer verticals few, extending only to top of eye; inner verticals and orbital setae absent. Clypeal setae 0-15. Palpal length less than width of face; second and third segment partially fused (Fig. 2). Antepronotum with medial commissure closed under scutal process (i.e., antepronotal halves not gaping) and only lateral setae present. Acrostichals absent. Dorsocentrals usually uniserial at mid-thorax but otherwise multi-serial. Prealars with some setae forward and free of main cluster. Scutellar setae numerous. Wing macrotrichia on cells absent but punctations gross and visible at X400; setae on R_{4+5} usually absent; anal lobe rounded; squama setae dark; alula without setae; venarum ratio 0.87-0.90. Spiniform setae of legs present only on 1st and 2nd tarsomere (ta) of P_2 and P_3; other leg setae finer. Ta_4 cylindrical and shorter or longer

than ta_5. Hypopygium with a rectangular sternapodeme. Sternite IX with a small tubercle protruding over base of each gonocoxite; anal point (AnP) absent or a small, awl-like protrusion of tergite IX which is not supported by oblique tergal apodemes. Pars ventralis small. Median volsella (MVo) clavate and setigerous; superior volsella (SVo) a strongly sclerotized and curving band (Figs. 3, 12). Gonocoxite tapering, nearly parallel sided, with longish setae scattered on the lower two-thirds; proximal half of inferior volsella (IVo) with a pile of microtrichia and distal half with short, perpendicular setae and ending slightly free of gonocoxite; and a second medial 'lobe' covered with short setae extending the length of the middle third of the gonocoxite. Gonostylus tubular, pubescent and with a few setae distally, terminally with thick chitin surrounding its face below the perpendicular macroseta, and two strong, perpendicular setae stand just proximal to macroseta (Figs. 3, 7).

Female.— Antenna with six flagellomeres (first two somewhat fused). Alula of wing with setae and anal lobe not rounded. Tergite IX apparently large, segment X without setae, lateral parts darkly sclerotized, postgenital plate apparently well developed, cerci hexagonal with subequal sides, and three oval seminal capsules. (Serra-Tosio 1971:Fig. 124; Saether 1977, based on *S. zavreli*).

Pupa.— Length 5-7 mm. Frontal apotome without cephalic tubercles, but long frontal seta arising from each rugose spot. Thoracic horn absent. Middle precorneal seta longer and thicker than the two, subequal, flanking setae. Thoracic, antennal and wing sheaths smooth. Leg sheath of P_3 ending in a Z-curve. Tergite I (TI) with only a polygonal pattern and only L_2 and L_4 present. Tergites II-VII with an anterior band of color only (apophyse) followed by some group shagreen bordering polygons; then spinulae dispersing evenly and ending in rows of small, triangular spines on the posterior margin; finally rows of strong, anteriorly pointing spines on conjunctiva II/III - VII/VIII (Fig. 4). L_2 dorsal. L_{1-3} evenly spaced but moving toward lateroposterior on each successive segment. L_3 and L_4 in close proximity. L-setae usually apically forked, up to eleven branches on L_2 on VII and VIII. D-setae small, dispersed, and usually simple. MD1 somewhat transverse and MD2 longitudinal. Shagreen on sternites similar to that of tergites. Segment IX with a fringe of very short setae on lateral border; each lobe having a terminal, tooth-like ventral tubercle near the last of the three straight macrosetae. Gonopodal sacs straight and not extending past caudal margin.

Larva (*4th stadium*).— Head quadrate, rather thinly sclerotized, and color uniform luteous or darker. Mentum with a yellow or smoky, subequally trisected ventromentum (median area) that is 6-7X the width of the much darker first dorsomental (lateral) tooth; six to seven

obliquely arrayed, dark lateral teeth. Ventromental plate (VmP) present, teardrop-shaped, or absent. Antennal AR 1.5 or 2.0-2.5; A_2 appearing very bifid with the blade base fused to it laterally, or appearing normal with the blade base fused to A_2 nearer to the apex of A_1; ring organ in basal fourth; blade and style elongate, reaching at least to A_4; A_3 annulate. Labrum with simple S-setae, mostly simple chaetae, and simple spinulae over premandible. SIII hairlike and SIV lanceolate. Labral lamellae (LL) two broad, simple or slightly denticulate plates. Chaeta media broad at base and sometimes frayed apically. Epipharyngeal area with a three scaled pecten flanked on each side by a pair of larger blades and several thinner spines. Premandible mitten-shaped with 1-4 inconspicuous lateral teeth on its medial, curved margin; brush spike-like lateral spine only. Mandible normal or sickle-shaped as in *Potthastia* spp. Prementum with three groups of long, flat bristles. Maxilla with a low palp and sensilla; galea without a row of lanceolate pegs. Body moderate in length (6-12 mm) and without conspicuous lateral setae even on the 10th segment (base of parapod). Procercus button-like, heavily sclerotized anally, height to width about one, and supporting seven long (about 400 um) anal setae (AS) and two small, unequal lateral setae. Supraanals not reduced, but shorter than anal setae. Anal tubules (TA) fingerlike, rounded or pointed apically, and shorter than parapod. Posterior parapod moderately elongate with 16 dark claws.

Remarks.— The adult males of *Sympotthastia*, according to Serra-Tosio (1971), is relatively plesiomorphic to *Potthastia* based on the trends of unreduced chaetotaxy and the cylindrical ta_4. Using the reduction in chaetotaxy within the genus, a phylogenetic scheme is proposed that includes the Nearctic species and that leaves *S. zavreli* the most apomorphic (Fig. 14).

Sympotthastia is a very uniform genus in all stages, but two species groups may be separated. The *zavreli*-group is mostly Palaearctic, and the *fulva*-group is Nearctic. Adults have differences in the palpal 2nd segment, color of capitellum of haltere, and anal point. Pupae show only slight variations in chaetotaxy, and larvae have or do not have ventromental plates and have differently shaped mandibular armature. Specifics are used in the following keys. Because of this homogeneity no subgeneral are proposed.

Ecology.— The temperate *Sympotthastia* species can be found in the peneplaned or filled valleys of the foothills-piedmont within the altitude of 60 to 220 m. The small streams of these lowland valleys originate in forested hills of about 350 m altitude, and they are secondarily cutting into the floodplain, exposing rock and sand substrate. They are moderately mineralized and relatively free of silt (and pollution). Surrounding land is used for moderate agriculture, or remains forested.

Larvae can be found in crude cases in pools or in reaches with laminar flow. Their guts contain predominantly diatoms. Flight time is from March to June when water reaches 10-15°C. This ecological summary was taken from Serra-Tosio (1971), Johannsen (1937), Pagast (1947), Ferrarese and Rosaro (1981) and conversations with U.S. Geological Survey personnel and with David Lenat of the North Carolina Department of Natural Resources and Community Development.

KEYS TO MALES, PUPAE AND LARVAE OF *SYMPOTTHASTIA*

MALES

1\. AnP awl-like, bare, 60-90 um long. Capitellum dusky. Palpal 3d segment without a keel of dark setae (*fulva*-gp.)....................................2

\- AnP absent or conical, hairy and one or two spines apically (Figs. 9-11). Capitellum clear. Palpal 3d segment expanded bearing a keel of dark setae (*zavreli*-gp.)....................................3

2\. AR 2.4-2.6; A_{13} 800 um long. LR 73, 49, 53; P_3 with ta_4 110 um and shorter than ta_5. Palpal length 500 um; palp to face about 85. Clypeal setae about 15. SVo straight distally (Fig. 13). Body and wing about 3 mm .... *S. fulva* (Joh.)

\- AR 2.7-2.9; A_{13} 995 um long. LR 88, 54, 52; P_3 with ta_4 170 um and longer than ta_5. Papal length 850 um; palp to face 87-98. Clypeals 12-15. SVo sigmoid (Fig. 3). Body 5-6 mm; wing 3.6 mm .... *S. diastena* (Subl.)

3\. AnP absent or minuscule and hairy. Clypeal setae absent. LR 81, 49, 59. AR 2.4-3.0; A_{13} 1150 um long. Palp to face 67-72. VR 85-92. SVo near Fig. 12, but lacking spinulae. Body 4-6 mm; wing 3-4 mm ... *S. zavreli* Pag.

\- AnP conical, hairy, and stong spine(s) apically. Clypeals present. LR 75, 52, 58 or 64. VR 87-90 4

4\. AnP about 35 um long with one spine apically (Figs. 7, 9, 10). Clypeals 4 or 5. Palp to face 79-85. AR 1.6-1.8; A_{13} 750 um long. SVo sigmoid, narrow, and smooth (Fig. 8). P_3 with ta_4 125 um long and LR 64. Body 4.3-4.8 mm; wing 3.5 mm .... *S. spinifera* Tosio

\- AnP longer with two unequal spines apically (Fig. 11). Clypeals 11. Palp to face 89. AR 3.0; A_{13} 1095 um long. SVo band-like with fine spinulae on surface (Fig. 12). P_3 with ta_4 195 um long and LR 58. Body 5.5 mm; wing 4.3 mm.................................... *S. macrocera* Tosio

PUPAE

1\. L-setae of VII-VIII subequal and not darker than those on preceding segments and L_2 with 8 branches or less. D_4 of III-VII larger than D_5 and sometimes bifid on VII or VIII. Shagreen near apophyse of TII weakly grouped. Thoracic spiracle (bulb) without spinulae. Coloration yellow-brown with transparent-brown setae and spines, and muscle scars clear or colored (*fulva*-gp.)....................................2

L-setae of VII-VIII shorter (by 1/3) and darker than those of VI and L_2 with more than 8 branches. D_4 of III-VII simple and subequal to D_5. Thoracic spiracle (bulb) with spinulae. Muscle scars dark (*zavreli*-gp) ...3

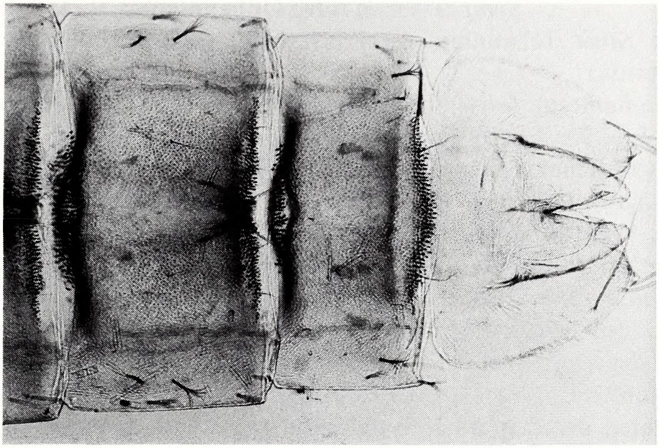


Fig. 4. *S. spinifera* from Italy, pupa. Typical of genus.

2. L_3 simple or bifid on III-VI. Muscle scars dark. Few spines on conjunctiva II/III .... *S.* sp. (Saether 1969)
- L_3 on II-VI simple. Muscle scars clear. Many spines on conjunctiva II/III .... *S. fulva* (Joh.)
3. L_3 on II-VI usually bifid or trifid and not much finer than the other L-setae. Macrosetae of IX subequally spaced. Shagreen near apophyse of II strongly grouped. Color pale yellow with darker areas .. *S. zavreli* Pag.
- L_3 on II-VI fine and usually simple, at most bifid. Anterior macroseta of IX noticeably separate from terminal pair (Fig. 4). Shagreen near the apophyse of TII weakly grouped. Color of abdomen II-VIII clear-brown with darker spines.. *S. spinifera* Tosio
  .... *S. macrocera* Tosio

LARVAE

1. Ventromentum yellow and VmP absent. Mandible with subequal lateral teeth set in as a group. Premandible with 1-2 small lateral teeth. Blade fused to mid-A_2. AS about 1.5X longer than supraanals (*fulva*-gp.) 2
- Ventromentum smoky colored; VmP present, teardrop shaped. Mandible normal; lateral teeth thorn-like, individual outgrowths. Premandible with about 3 inconspicuous lateral teeth. A_2 appearing less bifid as blade base is nearer to apex of A_1. AS 2X longer than supraanals (*zavreli*-gp.) 3
2. AR 2.2. Head capsule with flecks of chitinous thickening. Alaskan arctic .... *S.* cf. *fulva*
- AR 1.5. Head thinly sclerotized. New York .... *S. fulva* (Joh.)
3. AR 2.5. Blade reaching A_5. Premandible dark and with 2-3 lateral teeth. Ventromentum standing above laterals. LL two nondenticulate plates .... *S. zavreli* Pag.
- AR 2.2. Blade reaching A_4. Premandible dark and with 3-4 lateral teeth. First pair of lateral teeth projecting above ventromentum. Two LL, each with about 3 denticulations .... *S. spinifera* Tosio

Sympotthastia fulva (Johannsen)

Diamesa fulva Johannsen, 1921:229, orig. design. (holotype female description).

D. (*Psilodiamesa*) *fulva* Joh., Johannsen, 1937:33-34 (description of pupa, Fig. 91; description of larva, Figs. 92-96; keys; also noted that male and female imago descriptions were associated with the immature stages); Pagast, 1947:511-512, 569 (remarked that this species lies within *Sympotthastia*; Thienemann, 1952:248 (keyed it near *Potthastia gaedii*).

Psilodiamesa fulva Joh., Johannsen and Townes, 1952:13.

D. fulva Joh., Roback, 1957:51, 53 (keys); Sublette, 1964:129-130 (color description of a female that is perhaps this species); Sublette and Sublette, 1965:276 (distribution); Sublette, 1967:480-483 (supplemented description of female and male with accurate figures of male hypopygium).

Sympotthastia fulva (Joh.), Saether, 1969:34 (description of a probable new species near this one); Serra-Tosio, 1971:281 (placement within genus near *S. spinifera*); and Hansen and Cook, 1976:142 (generic placement).

Larva.— Head yellowish and thinly sclerotized without flecks of reinforcing chitin. Mentum as described for genus; specifically, ventromentum yellow and VmP absent. AR 1.5; A_1 length/width (ALAW)= 3; antenna to mandible 6:10. Contrasted to *S. zavreli* below, the SI is shorter, wider and more blade-like; SII subequal to SIII; LL two non-denticulate plates. Premandible with 1-2 lateral teeth. Mandible as in *Potthastia* spp., i.e., somewhat sickle-shaped, toothed area dark, and four, subequal laterals set in as a group. Si with 20 finely serrated branches, proximal ones longest. Maxilla as in Johannsen (1937: Fig. 94). Body 7 mm. Procercal height/width (H/W)= 0.8. Seven AS, 1.5X longer than supraanal setae. TA three-fourths the length of parapod. Posterior parapod with the nominal 16 claws (*versa* Johannsen 1937:33).

Material.— USA: New York, *Tompkins Co.*, Cascadilla Cr. at Cornell Univ., Ithaca. Paratype female, pinned; allotype male hypopygium and antenna and pupal and larval skin, Cornell Univ. no. 2326, slide mounted (specimens squashed), and the remainder of the pinned male was slide mounted in Euparal.

Sympotthastia cf. *fulva* (Joh.)

Larva (4th stadium, N=1).— Fig 6. Head rather robust, brown with flecks of heavier sclerotization. AR 2.2; blade fused nearer to base of A_2 than in *fulva*, resembling *zavreli*. Body length and color indeterminate. Remaining characters identical to that of *fulva*.

Material.— USA: Alaska, Happy Valley Cr. (Sagavanirktok R.

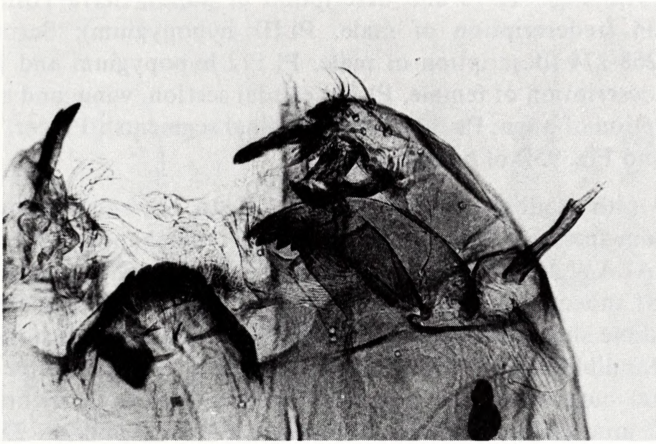


Fig. 5. *S. zavreli* from North Carolina, larval head.

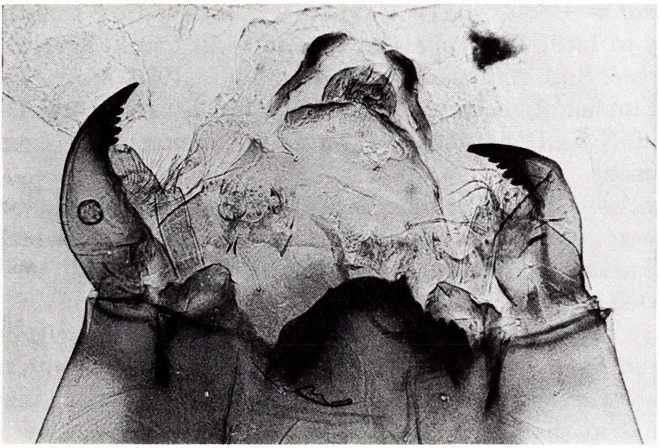


Fig. 6. *S.* cf. *fulva* from Alaska, larval head.

basin) nr. Sagwon, 69°09′N 148°50′W, 7 July 1976. 4th stadium larva.

Ecology.— This specimen was drift-netted in an arctic creek with abundant orthoclads, simuliids and baetids. The following parameters were noted for this creek a few years earlier: June - Sept. 1972, temp. to 11°C, conductance very low, pH circumneutral, alkalinity 12-18mg/1, discharge 1-1.5m³/s (Nauman and Kernodle 1973).

Sympotthastia zavreli Pagast

Syndiamesa sp. Thienemann, 1934, in the keys of Johannsen (1937) and Roback (1957).

Sympotthastia zavreli Pagast, 1947: 458-459 and 510-512 (description of

male with Figs. 12-15 and description of pupa); Serra-Tosio, 1968: 130-134 (redescription of male, Pl.III hypopygium); Serra-Tosio, 1971:268-274 (description of male, Pl.122 hypopygium and Pl.123.1 SVo; description of female, Pl.124 caudal section, wing, and antenna; description of pupa, Pls.125-126 abdominal segments); Pinder, 1978:44 (key and Fig. 95B of hypopygium).

Larva (4th stadium, N=2).— Fig. 5. Head brownish-yellow. Ventromentum smoky in color. VmP clear, teardrop shaped. Antennal AR 2.2-2.5; ALAW 4-5. Antenna to mandible 6:10. Labral S-setae all strong spines. SI subequal to SII; SIII hairlike. LL two nondenticulate plates. Premandible short and darkened distally with 2-3 inconspicuous lateral teeth. Mandible normal with each of the four lateral teeth appearing as individual outgrowths. Si with 12-17 nearly smooth branches. Body about 11 mm. Color brownish. Procercal H/W= 1.0 and AS 2X longer than supraanals. TA rounded or pointed distally and nearly half the parapod length.

Material.— USA: North Carolina, *Durham Co.*, simipermanent tributary to Little R.; *Wake Co.*, trib. to Swift Creek. Several 4th stadium larvae. Both stations were sampled 5 Feb. 1980. *Moore Co.*, Deep Creek (Lumber R. basin) 9 Feb. 1982. One larva. All leg. D. Lenat; collection N.C. Department of Natural Resources and Community Development.

Remarks.— These Carolina specimens obviously do not belong to the *fulva*-gp. by diagnosis since this species has ventromental plates. Although unassociated, they fit no known species description but that of *S. zavreli* (cf. Thienemann 1952).

Ecology.— The Carolina specimens were found with *Paraphaenocladius* and *Eukiefferiella* (b.s.) in small Piedmont streams with sand and gravel substrate and slow current. Thienemann (1952) stated that *zavreli* was found in shallow, unshaded trout streams having slow current, spring runs, and meadow ditches, and that diatoms were prevalent in guts. These new Nearctic finds had consumed mostly *Synedra* and *Gomphonema*.

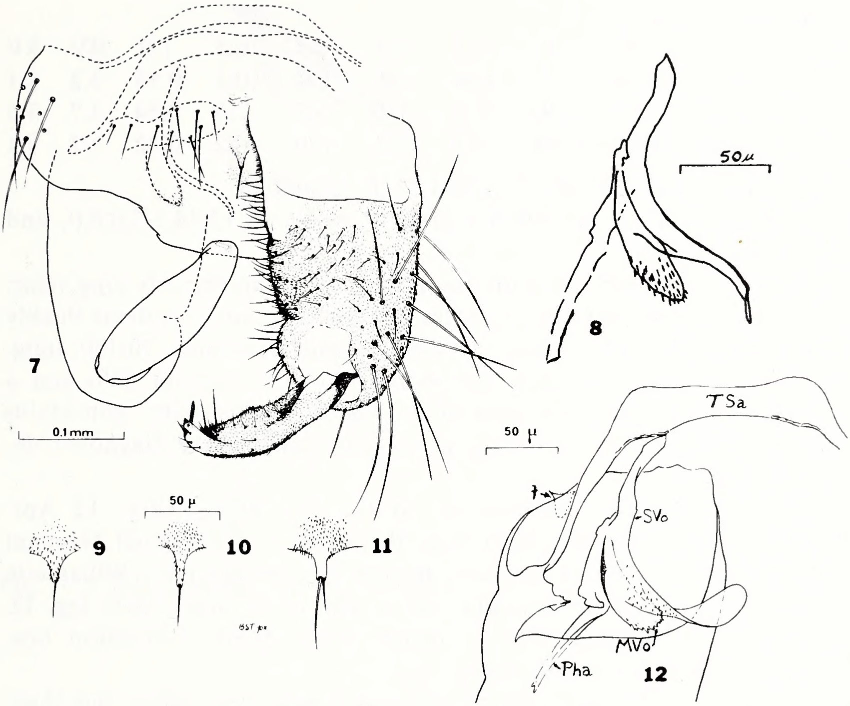
Sympotthastia diastena (Sublette) *comb. n.*

Pseudodiamesa (*P.*) *diastena* Sublette, 1964:128, orig. design. (Fig. 7b,c of male hypopygium and description of allotype).

P. diastena Sublette, Serra-Tosio, 1976:135 (stated placement questionable.

Sympotthastia diastena (Sublette), Dr. D. Hansen in 1973 determined two slide mounted males.

Male (N=2).— Figs. 1-3. The holotype was decidedly smaller than the following described specimens (measurements of holotype in paren-



Figs. 7-10. *S. spinifera* (cf. Serra-Tosio, 1971): 7, hypopygium; 8, phallapodeme; 9-10, anal point.
Figs. 11-12. *S. macrocera* (cf. Serra-Tosio, 1971): 11, anal point; 12, phallapodeme. Labels added: MVo, median volsella, Pha, phallapodeme, SVo, superior volsella, t, tubercle of SIX, and TSa, transverse sternapodeme.

theses). Unspecified lengths are in micrometers. Body length 5.7-6.0 mm (holotype 2.9 mm); wing 3.6 mm (2.9 mm). Coloration of head, body, wing veins and coxae dark; haltere dark, pubescent with capitellum somewhat lighter. Extremities of the legs and the sternites lighter.
Antennal flagellomere lengths: A_1 73-80 (60): A_{2-12} 24-27: A_{13} 995 (880). AR 2.7-2.9. A_{3-12} width greater than length, excepting the last few which become squarish. Width of head at eyes 750-820. Clypeus with 12-15 setae proximally in a staggered double row. Palpal segment 2-5 lengths: 105 (70): 220-280 (195): 250-280 (205): 295 (230). Antepronotum with 14 lateral setae: dorsocentrals variable — staggered single to triple row of 25-30 setae (holotype with a single to double row of 22 setae); prealars with a main cluster of 15 and anteriorly 7-8 isolated setae staggering forward (holotype with only 4 or 5 isolated setae). Scutellum with numerous setae. Wing VR 0.88. One specimen with a full row of setae on R_{4+5} (Fig. 1).

Leg segment lengths:

—	fe	ti	ta1	ta2	ta3	ta4	ta5	LR	BV	SV
P1	1426	1674	1472	628	426	194	163	0.88	3.2	2.1
P2	1542	1581	876	473	310	147	155	0.54	3.7	3.6
P3	1814	2030	1240	643	395	170	162	0.52	3.7	3.1

Tibial spur lengths: P_1 90, P_2 71 and 72, P_3 62 and 96.
Spiniform setae of $ta_{1\text{-}5}$ often paired: P_1 none, P_2 12-14,2-3,0,0,0, and P_3 13-16,2-5,0,0,0.
Tergite IX with each half with two groups of 6-8 moderately long setae; anal point naked, awl-like, 70-90 long. Transverse sternapodeme thickly rectangular. Straight coxite portion of phallapodeme, 70-170 long, articulating with a strongly sclerotized, narrow, sigmoid SVo and a membranous, ovate, setigerous MVo (Fig. 3). Gonocoxite, gonostylus and other details typical for the genus, and found in the diagnostic description above.

Material.— USA: CALIFORNIA, *Marin Co.*, Mill Valley. 12 Apr. 1957. Leg. H. L. Mathis, light trap. Holotype, U.S. National Museum no. 65522 (poor mount). OREGON, *Benton Co.*, Berry Creek (Willamette R. basin), 9 mi N of Corvallis, 60 m alt. 17-24 Mar. 1960, leg. D. Hansen; det. Hansen, 1973. 2 males. Univ. Minn. Collection nos. DH69-280 and -281 (in balsam?).

Remarks.— The holotype of *diastena* is very near *fulva*, but these new specimens show *diastena* can be much larger and darker than *fulva*. I doubt *fulva* will be found in the western Cordilleran. The numerous dorsocentral setal rows and forward running prealars, and the unique presence of setae on R_{4+5} (Fig. 1), demonstrate that this species is the most plesiomorphic species known in *Sympotthastia*. Its SVo is identical to *spinifera* and differs slightly from *fulva*.

The presence of a species different from *fulva* in the western Cordilleran is also demonstrated by the pupa found in Waterton National Park, Alberta, by Saether (1969) and keyed here as *Sympotthastia* sp. Also, the larva from the Alaskan arctic, *S.* cf. *fulva*, is separable. It may be that these unconnected metamorphic stages represent a single Cordilleran species.

Sympotthastia spinifera Serra-Tosio

S. spinifera Serra-Tosio, 1968:134-140, orig. design. (Figs. 1-4 of hypopygium; ecology); Serra-Tosio, 1971:224-227 (Pl. 123.2 phallapodeme; Pl.127 hypopygium; Pls. 128-129 pupa; p.277 ecology); Ferrarese and Rossaro, 1981:77-80 (larva description, Fig. 36 with mentum, labrum, antenna, premandible, procercus; pupal description, Fig. 37).

Sympotthastia macrocera Serra-Tosio

S. spinifera forma macrocera Serra-Tosio, 1968:137-138.

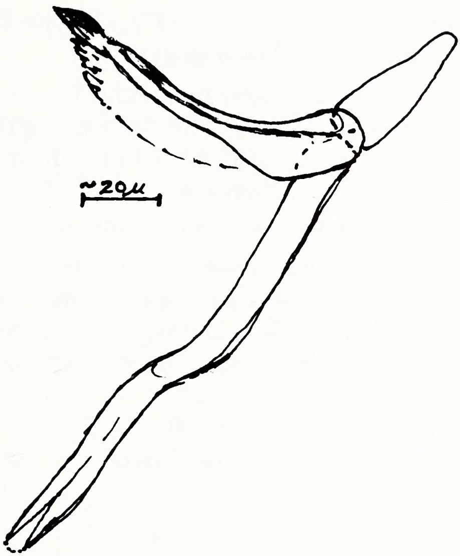


Fig. 13. *S. fulva*, phallapodeme of allotype no. 2326.

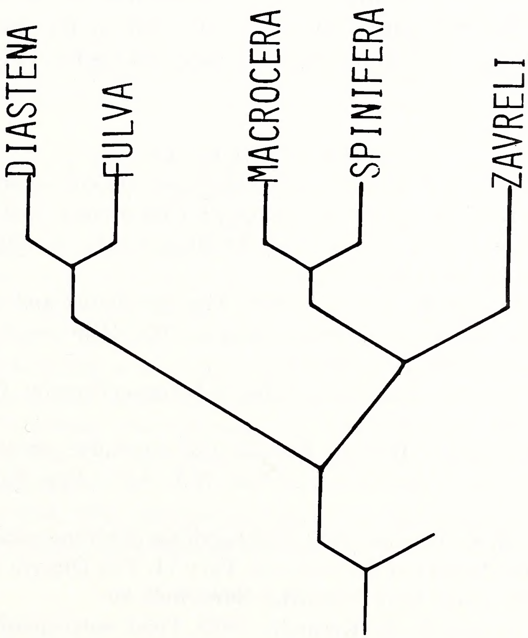


Fig. 14. Proposed cladogram of *Sympotthastia*.

S. macrocera Serra-Tosio, Serra-Tosio, 1971:277-280 (Pl.130 phallapodeme, gonostylus, and $ta_{3\text{-}5}$; p.279 ecology).

Sympotthastia sp. Saether

The two pupal exuviae (Saether 1969:34) were examined from Dr. Saether's collection. This species differs from *fulva* by having only a few anteriorly pointing spines on conjunctiva II/III. The lengths of these specimens were about 5 mm instead of the 8 mm reported by Saether.

Sympotthastia virendri (Singh)

This oriental species was placed in *Sympotthastia* by Sublette and Sublette (1973). I am inclined to think this is not suitable, since Singh (1958) described the species with hairy wings, pictured wing without strong anal lobe, with acrostichals, and, in a diminutive drawing, the SVo appears to be that possessed by the Diamesae. The number of spermathecae was not mentioned for the female described.

ACKNOWLEDGMENTS.— I thank the curators, Drs. Q. E. Wheeler, Paul Clausen and W. W. Wirth, for their efforts that allowed me to see important types, North Carolina's environmental biologists, and Drs. Bruno Rossaro and L. C. V. Pinder who loaned me Palaearctic examples. Special appreciation is extended to Dr. Bernard Serra-Tosio for allowing me to reproduce his excellent figures (Figs. 7-12).

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Genetic Variation in the Eastern Cottonmouth, *Agkistrodon piscivorus piscivorus* (Lacépède) (Reptilia: Crotalidae) at the Northern Edge of its Range

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ABSTRACT.— Genetic variation was examined by electrophoresis in six populations of *Agkistrodon p. piscivorus* from the northern edge of the species' range in southeastern Virginia. Twenty-three presumptive loci were found to be monomorphic, while three loci were polymorphic in some populations. Average observed heterozygosity values ranged from 0.9% to 2.9%, with a mean for all populations of 1.6%. Nei's index of genetic identity reveals that all Virginia populations sampled have a very high degree of genetic similarity, with a minimal value of .964.

INTRODUCTION

Advances in biochemical techniques have enabled researchers to collect a great deal of information on the amount of genetic variation that occurs in natural populations (Selander and Johnson 1973). Most of the studies dealing with snakes have involved the family Colubridae (Sattler and Guttman 1976; Gartside et al. 1977). Those studies that included species of the family Crotalidae analyzed only components of the venom.

The Eastern Cottonmouth, *Agkistrodon piscivorus piscivorus* (Lacépède), occurs primarily in the Coastal Plain of the eastern United States, where it ranges from Alabama to its northern distributional limits in the southeastern corner of Virginia. For years, the James River was thought to mark the northernmost limit for this species, just as it does for a number of other reptiles and amphibians (Wood 1954; Conant 1975). Cottonmouths, however, occur north of the James River in the vicinity of the Newport News-Hampton area (Engeling 1969; Linzey and Clifford 1981).

The distribution of the cottonmouth in Virginia is discontinuous. There is an isolated population along Swift Creek and the Appomattox River just west of Hopewell in Chesterfield County. "This population is at least 60 km from the nearest known locality in the main part of the range. . ." (Blem 1981:117). Populations of this species on the barrier beaches along Back Bay are separated from the mainland by several miles of water. Other populations, such as that at Sea Shore State Park,

are essentially isolated by "urban sprawl". Thus, there appear to be a number of potential barriers to gene flow in populations of this species in Virginia.

Several other species of snakes whose northern limits are essentially restricted to the Coastal Plain of southeastern Virginia also occur on the peninsula between the James and York rivers. They include the Timber Rattlesnake, *Crotalus horridus*; the Brown Water Snake, *Nerodia taxispilota*; the Redbelly Water Snake, *Nerodia erythrogaster erythrogaster*; and the Glossy Crayfish Snake, *Regina rigida rigida* (Linzey and Clifford 1981).

The distribution of such populations is open to two interpretations. The first is to assume that populations occurring north of the James River were established by animals that crossed the river in the same area despite its width (approximately 6 km). The second hypothesis is to assume that all of these species once occurred throughout the Coastal Plain of southeastern Virginia. This would enable colonizers to invade areas north of the James by crossing in the general vicinity of the Fall Line, where the river is a less formidable barrier. Subsequent elimination of intervening populations would then produce the distributional patterns currently observed. The potential isolation of populations could result in genetic differentiation due to lack of gene flow.

In this study, I used electrophoresis to examine genetic variation in several populations of *A. p. piscivorus* to determine: 1) levels of genetic variation that might accompany potential isolation; and 2) if patterns of genetic variation reveal any insights into the origin of populations of *A. piscivorus* north of the James River.

MATERIALS AND METHODS

Specimens collected in the field from May 1980 until September 1982 were returned to the laboratory and sacrificed by freezing. Attempts were made to collect specimens from every drainage system in Virginia where the species has been recorded. Localities where snakes used for this study were collected (Fig. 1) are: 1) Newport News Reservoir, Newport News; 2) Appomattox River near Hopewell; 3) Sea Shore State Park, Virginia Beach; 4) Gum Swamp near North Landing River, Virginia Beach; 5) Northwest River, Chesapeake; and 6) False Cape State Park, Virginia Beach.

Prior to electrophoresis, specimens were thawed and extracts of soluble proteins prepared by homogenizing samples of heart, liver, and skeletal muscle with equal volumes of 2% 2-phenoxyethanol. Homogenates were centrifuged at 4,000 G for 30 minutes. Supernatants were then decanted and used for electrophoresis.

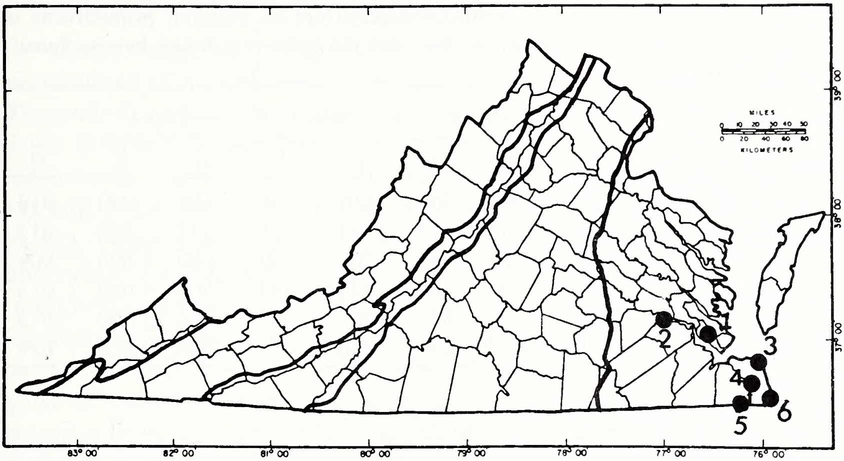

Fig. 1. Populations of *A. piscivorus* sampled for electrophoretic study. 1 = Newport News, 2 = Hopewell, 3 = Sea Shore State Park, 4 = Gum Swamp, 5 = Northwest River, 6 = False Cape State Park.

Starch gel electrophoretic techniques using the basic procedures of Selander et al. (1971) were used with the following modifications: albumin, hemoglobin, general proteins, and esterases were best demonstrated on the Poulik buffer, while all other enzymes were isolated on gels using the Tris-Maleic acid buffer. All gels were 12.5% starch (Electrostarch Lot 307, Otto Hiller, Madison, Wisconsin).

Isozymes of various proteins were designated in order of decreasing anodal mobility. Alleles present at polymorphic loci were designated alphabetically by a superscript following the locus designation. Nei's (1972) index of genetic identity was used to compare genetic similarities between populations, and mean heterozygosity per individual ($\bar{H}$) was calculated for each population.

RESULTS

Of the 29 protein loci examined in this study, 23 were found to be monomorphic in all individuals examined. These loci included: albumin, hemoglobin, three general proteins, three esterases, two malate dehydrogenases, two lactate dehydrogenases, two phosphoglucomutases, one phosphoglucose isomerase, α-glycerophosphate dehydrogenase, glutamate dehydrogenase, two superoxide dismutases, isocitrate dehydrogenase, 6-phosphoglucose dehydrogenase, sorbital dehydrogenase, and glutamate oxaloacetate transaminase (Got-1). Only three loci were polymorphic; their gene frequencies are listed in Table 1.

Table 1. Allelic frequencies at polymorphic loci in Virginia populations of *Agkistrodon piscivorus*. N = sample size; $\bar{H}$ = mean heterozygosity per individual.

		Got-2		Xdh-1		Lap-1		
Locality	N	a	b	a	b	a	b	$\bar{H}$
1. Newport News	10	.300	.700	.850	.150	.100	.900	.019
2. Hopewell	9	.111	.899	.944	.056	.111	.889	.017
3. Sea Shore	2	.250	.750	.000	1.000	.000	1.000	.009
4. Gum Swamp	7	.214	.786	.857	.143	.000	1.000	.013
5. Northwest R.	11	.364	.636	.091	.909	.000	1.000	.012
6. False Cape	10	.400	.600	.350	.650	.000	1.000	.029

Variability at Polymorphic Loci

Got-2: This locus was polymorphic in all populations, with the frequency of Got-2^a ranging from .111 in the Hopewell population to .400 in the False Cape State Park population.

Xdh-1: Two alleles were present in all populations, with the exception of Sea Shore State Park where only Xdh-1^b was present. Xdh-1^b was the predominant allele in the False Cape State Park and Northwest River populations, while Xdh-1^a predominated in the populations from Hopewell, Newport News, and Gum Swamp.

Lap-1: Most individuals were monomorphic for Lap-1^b, but one individual from both Newport News and Hopewell populations possessed Lap-1^a in the heterozygous condition.

Observed mean individual heterozygosity values ($\bar{H}$) ranged from a low of 0.9% in the Sea Shore State Park population to a high of 2.9% in the population at False Cape State Park. The mean heterozygosity per locus per individual for all populations was 1.6%. Nei's (1972) index of genetic identity values for all pairings is presented in Table 2.

Table 2. Nei's index of genetic identity values between populations of *Agkistrodon piscivorus* from Virginia.

	Newport News	Sea Shore	Gum Swamp	Northwest River	False Cape
1. Hopewell	.99826	.97109	.99932	.97664	.98925
2. Newport News		.96390	.99880	.96840	.98229
3. Sea Shore			.97118	.99918	.99434
4. Gum Swamp				.97601	.98847
5. Northwest R.					.99731

DISCUSSION

The average heterozygosity value of 1.6 reported here for Virginia populations of *A. piscivorus* is less than that of 4.1% - 8.3% reported for *Thamnophis sirtalis* by Sattler and Guttman (1976), and the 9.2% and 7.7% reported for *Thamnophis proximus* and *Thamnophis sauritus*, respectively, by Gartside et al. (1977). It is interesting to note the extremely low heterozygosity in the Sea Shore State Park population (0.9%). Virginia populations of *A. piscivorus* appear to exhibit less variation than other species of snakes. Two specimens of the Florida Cottonmouth, *Agkistrodon piscivorus conanti*, were found to be almost identical to Virginia specimens based on electrophoretic analysis of the same loci. Only the presence of a unique allele at the Got-1 locus distinguished it from Virginia *A. piscivorus*. Since there is so little variation between these two subspecies, the low amount of variation and heterozygosity reported in this study may be typical for the species. Thus, *A. piscivorus* may have had a rather conservative biochemical evolution, if we can draw inferences from data at hand.

The highest level of heterozygosity was observed in the population at False Cape State Park (2.9%), while the lowest was seen in the Sea Shore State Park sample (0.9%). This population is unique in that housing developments separate it from other populations. The surrounding area is one of the most rapidly developing areas in the United States. Although the park once supported high-density populations of cottonmouths, the species has become extremely rare there in recent years. Despite extensive field efforts over a two-year period, only two specimens were collected. This apparent decline may be an effect of the extensive droughts this area has suffered during the past few years.

Nei's (1972) index of genetic similarity reveals all populations are extremely close genetically. Even the lowest pairing value (.964), obtained in comparing Sea Shore State Park with the Newport News population, indicates a very high degree of genetic similarity among all Virginia populations sampled. Although all Virginia populations of *A. piscivorus* sampled are very similar genetically, the Hopewell, Gum Swamp, and Newport News populations show the highest values for genetic similarity. All three displayed a very high frequency for Xdh-1^a, which occurred in much lower frequencies in the other populations and was absent from the Sea Shore State Park samples. While the Newport News population shared a slightly higher identity with the Gum Swamp population than with the Hopewell population (.99880 vs .99826), this extremely small difference can be explained by the very low frequency of Got-2^a (.111) and higher frequency of Xdh-1^a (.944) in the Hopewell population. Both of these loci appear to be heading towards complete fixation of alleles, either by selection or by drift, in this isolated population. Such patterns

have been observed in isolated populations of other species (Avise 1976). Fixation of Xdh-1^b in the Sea Shore State Park population also appears to be in progress. Additionally, the presence of Lap-1^a in only the Hopewell and Newport News populations indicates the close genetic relationship between them. This suggests that the populations of *A. piscivorus* north of the James River are derived from populations in the vicinity of Hopewell rather than farther down the river. This hypothesis is supported by other species of snakes with distributions similar to that of the cottonmouth. *Nerodia taxispilota* occurs on the Peninsula, but does not extend to its lower end. The single Virginia record for *Regina r. rigida* is also from the uppermost reaches of the Peninsula. Whether this represents a relict population or a short-lived introduction is problematical. While these species would be able to cross the James River at its widest expanse, they are absent along the river in its lower reaches.

The distribution of the species least likely to cross large expanses of water, *C. horridus*, lends further credence to the hypothesis. The timber rattlesnake has a more extensive distribution on the Peninsula than does the cottonmouth, but it also is not recorded from the counties directly below the James River. Yet there are records for this species from Prince George County, very near the Hopewell population of *A. piscivorus*. Both *N. taxispilota* and *N. e. erythrogaster* also persist in this same general region.

The elimination of intervening populations for these species may be a result of climatic factors, at least in the case of *A. piscivorus*. It appears that the distributional range of this species in Virginia is contracting. Richard Hoffman (in Russ 1973) reported that cottonmouths were once common east of the Fall Line in Virginia, but are now only rarely found in many areas. Today, even in the Dismal Swamp, the species is so rare that the Park Service will not issue permits to collect this species. Many areas that once supported large populations no longer do so, and it appears that the range of this species is being pushed to the southeast. Blem (1981) felt that the record cold winters during the last decade may have had a decimating effect on the survival of this species at the northern edge of its range.

In summary, it appears that the levels of genetic variation observed in six Virginia populations of *A. piscivorus* are lower than those reported for other snakes. This species and several others of the Coastal Plain probably had more extensive distributions in the past, but appear now to be undergoing range contractions. Virginia cottonmouth populations that still seem to be thriving also display the highest genetic variation.

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Seasonal Weight Changes in Raccoons (Carnivora: Procyonidae) of North Carolina

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ABSTRACT.— Raccoons, *Procyon lotor* L., were studied in North Carolina to determine if seasonal changes in body weight occur in this species in a mid-latitude region. The sample consisted of live-trapped animals and intact carcasses from a fur buyer. Juvenile male body weights increased from the end of July to mid-December 1975. Body weights of juvenile males and females tended to decline between mid-December 1975 and February 1976. During the midwinter of both 1975 and 1976, adult male and female body weights decreased; the decline was less extreme and occurred about two weeks later than declines reported for the northcentral United States. This pattern of weight loss at higher latitudes may reflect the greater energetic cost of raccoon winter foraging at northern locations. Such sites experience lower temperatures than more southerly sites, and their ground vegetation is less accessible because of deeper snows.

INTRODUCTION

Systematic seasonal changes in body weight occur in a variety of nonhibernating mammals (for examples see Keller and Krebs 1970; Markham and Whicker 1973; Iverson and Turner 1974; Mautz 1978). This is not surprising since food quality and/or quantity normally vary within a year. Except for those of Iverson and Turner (1974) and Mautz (1978), most reports of such seasonal weight changes are presented without ecological explanations, or as events associated with population cycles (e.g., Keller and Krebs 1970). In this study we examined raccoons, *Procyon lotor* L., in North Carolina to determine whether such changes occur in this species in a mid-latitude region. Seasonal body weight changes have been documented in raccoons from the northern (Stuewer 1943a; Mech et al. 1968) and southern (Johnson 1970) United States. Thus, we could also evaluate geographic variation in this phenomenon.

METHODS

This study was conducted in the North Carolina piedmont from January 1975 through February 1976. Study areas included the Ecologi-

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cal Research Area of North Carolina State University (NCSU), 3.2 km southwest of Raleigh, and woods in two nearby locations: Schenck Forest and the Faculty Club, both of NCSU.

Live traps baited with sardines and corn were placed along stream bottomlands and checked daily. Twenty-two captured raccoons were restrained in a wire cone (Stuewer 1943b), weighed (±1.0 g), measured (±0.5 mm), sexed (Stuewer 1943b), ear tagged, and released. Additional data were obtained from 123 intact carcasses from a fur buyer in Smithfield, 48.3 km south of Raleigh. All of these raccoons were trapped within a 150 km radius of Smithfield less than two weeks prior to examination (L. Barbour, pers. comm.). Exact capture dates were not known for about 75% of the specimens. As approximations used to compute regressions of body weight over time, dates for these animals were estimated to be seven days prior to the date of necropsy.

The dead raccoons were aged by degree of epiphyseal closure seen in X-rayed radii and ulnae (Sanderson 1961). We analyzed the data from the noncastrated raccoons in Sanderson's (1961:9) Illinois sample and found that the mean ages of females with broad, thin, and closed epiphyses were all significantly different ($P<0.01$) with little overlap between the means' 95% confidence limits. Since these means corresponded nicely with year classes, we categorized our females with broad epiphyses as juveniles (≃ zero-one yr), with thin epiphyses as subadults (≃ one-two yr), and with closed epiphyses as adults (≳ two yr). In Sanderson's study, the only significant difference ($P<0.01$) was between the mean ages of males with broad and thin epiphyses. Again, matching epiphyseal closure with mean age, our males were classified as juveniles (≃ zero-one yr) or adults (≳ one yr). Fifty raccoons, including those live-trapped, were not X-rayed. Instead, they were assigned to age classes by comparing their total lengths and body weights with the means and 95% confidence intervals of these variables displayed by the animals we did X-ray.

Weights of males and females were plotted separately against dates by age. We noted that weight typically increases during the fall or early winter through December, and is followed by a midwinter decrease. Weights of juvenile males increased by midsummer. Stepwise regression analyses were used to determine if these visually observed changes were statistically significant.

RESULTS AND DISCUSSION

Although adult weights decreased during January and February of 1975 and 1976, the only statistically significant change was for males in 1975 ($r = -0.45$; $P<0.05$; $N = 20$). However, since the pattern was consistent in both sexes each year, it appeared real and justified data pool-

ing. Slopes and intercepts of the descending lines of adult male body weight in January and February were similar in 1975 and 1976 ($P>0.05$, F-test); the same was true of adult female body weights. The negative slope of the pooled male sample was significant ($r = -0.45$; $P \cong 0.01$; $N = 30$) and the pooled female data also provided a clearly decreasing body weight trend ($r = -0.44$; $P \cong 0.08$; $N = 18$). These adult weight decreases in January and February were compared between sexes (F-test). Slopes were similar ($P>0.05$) but intercepts were not ($P<0.01$), with males being typically heavier.

In Minnesota, Mech et al. (1968) reported a 50% weight decline in adult raccoons from late November through mid-March followed by a weight gain beginning in mid-April. Adult raccoon weights were also found to be minimal in the spring in Michigan (Stuewer 1943a) and Alabama (Johnson 1970). In Alabama, however, spring weights were only about 20% less than those in the fall. We also found this midwinter weight decline to be less extreme in North Carolina. In the pooled sample regressions, expected values of adult weight decreased by 22% for males and 27% for females through January and February. Further, this winter decline in adult raccoon weights begins about two weeks later in North Carolina than it does in the northcentral states (see Stuewer 1943a; Mech et al. 1968).

Body weights of juvenile male raccoons increased from the end of July to mid-December 1975 ($r = 0.71$; $P<0.05$; $N = 12$), followed by an insignificant decreasing trend through February 1976 ($r = -0.43$; $P>0.05$; $N = 5$). Juvenile female weights also declined from mid-December 1975 through February 1976 ($r = -0.65$; $P \cong 0.06$; $N = 9$). Similarly, both Stuewer (1943a) and Mech et al. (1968) found that body weights of juvenile raccoons in Michigan and Minnesota increased until November of their first year and then declined. We also observed yearling female weights to increase from November 1975 through January 1976 ($r = 0.85$; $P \cong 0.08$; $N = 5$), another pattern consistent with those found farther north by these authors.

Iverson and Turner (1974) suggested that mammals lose weight when it is adaptive to lessen energy requirements in certain seasons. However, a weight decrease normally occurs by fat loss, which need not imply lower energy requirements. Energy demands could even be relatively high in fat depleted individuals. For example, raccoon weights are lowest by winter's end, a time when energy requirements for upcoming breeding events should be high.

We suggest a less complicated explanation, which is simply that animals put on weight while food is readily available to prepare them for the harsher winter and early spring. Mautz (1978) argued that white-tailed deer, *Odocoileus virginianus*, add fat in summer and fall to offset

the lower nutritive value of winter browse. Both situations are, of course, analogous to that occurring in many hibernators (e.g., Davis 1976). In raccoons, fat stores would become depleted in winter because of (1) higher metabolic costs of staying warm, (2) more energetically expensive foraging associated with greater reliance on predation (Johnson 1970), which is a more active type of foraging, and (3) reduced overall food intake because of sparser food sources. Northern latitudes, with colder temperatures and vegetation made less accessible by deeper snows, should be the most energetically demanding places for raccoons in the winter. This would explain the latitudinal differences in adult weight loss. Other comparisons support this explanation. The periods of yearling weight increase and adult weight decrease occur later in North Carolina than in the northcentral states and are less extreme. Where winter arrives later and is not as harsh, weight gains need not occur as early to ensure survival. Instead, energy stores that last longer into the winter should delay weight loss.

Winter foods of raccoons might be of low nutritive value. But, since raccoons are extremely omnivorous, this should be less a factor in their weight changes than for those in obligatory herbivores like deer (see Mautz 1978). Furthermore, since raccoons exhibit denning behavior and often forage at night, when winds are typically less severe, they might have lower winter energy demands per unit weight than deer. Certainly, other factors such as the insulative quality of the fur and physiological adaptations also need to be considered for a valid comparison to be made.

Finally, breeding activity in the later winter and early spring might influence the pattern of adult raccoon weight decrease by causing a further drain on fat stores. In a separate study (Zeveloff and Doerr 1981) we found a high negative correlation between mean body weights and mean testis weights of 16 adult male raccoons from mid-January through February 1976 ($r = -0.99$; $P<0.01$). This indicates that male body weight decreases at a time of increased reproductive activity. To fully understand raccoon body weight dynamics, one might consider their reproductive events in addition to geographic variation in climatic seasonality and food availability.

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Age, Growth, Food Habits, and Reproduction of the Redline Darter *Etheostoma rufilineatum* (Cope) (Perciformes: Percidae) in Virginia

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ABSTRACT.— Life history aspects of *Etheostoma rufilineatum*, the redline darter, were investigated from May 1981 to May 1982 in the North Fork Holston River, Virginia. Analysis of scale samples indicated that males and females grew at approximately the same rate, but males reached a greater maximum length. Estimated annual survival rate for age II and older males was 0.28 and for females 0.03. Aquatic insect larvae were the major food items, and dipterans predominated numerically (68-87%) year-round. Feeding over a 24-hour period peaked from early to late afternoon (1600-2000 hr). The sex ratio favored males throughout the year (2.5:1) and was attributed to differential survival and distribution. Age I fish more than 42 mm long, of both sexes, were sexually mature. Ripe males were first collected in March, although spawning coloration was evident in December. Female ovaries began maturing in late February, and spawning occurred from mid-May to mid-August.

INTRODUCTION

The darters are small members of the family Percidae and constitute a diverse group of North American fishes, with 145 species in 3 genera and 28 subgenera (Collette 1967; Page 1983). They reach maximum lengths of 35-200 mm and differ widely in morphological characteristics, habitat preference, and behaviors. A comprehensive review of the biology and ecology of darters was published by Page (1983).

The redline darter, *Etheostoma rufilineatum* (Cope), is one of 13 species in the subgenus *Nothonotus*, one of the more gaudy groups of darters. *Nothonotus* species exhibit strong sexual dimorphism. Males of most species display brilliant coloration during most of the year. The species occur in riffle habitats of clear upland streams. Most occupy the

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Ohio River basin, but one species occurs in direct tributaries of the lower Mississippi River, one in the Mobile Bay drainage, and two in the Ozarks. Of the 13 species, life history studies have been conducted only on *Etheostoma acuticeps* Bailey, the sharphead darter (Jenkins and Burkhead 1975; Bryant 1979) and *Etheostoma maculatum* Kirtland, the spotted darter (Raney and Lachner 1939), and comparative ecological studies were done on 3 species (Stiles 1972).

The redline darter occurs in tributaries of the Tennessee and Cumberland rivers in Virginia, North Carolina, Tennessee, Kentucky, Georgia, Mississippi, and Alabama (Etnier 1980). It is found in swift, shallow riffles of clear streams and may exist in riffles shallower than those preferred by other *Nothonotus* species (Zorach 1970). Except for studies on systematics (Zorach 1970) and breeding and food habits of three *Nothonotus* species (Stiles 1972; Bryant 1979), no biological information is available on the redline darter. The present study was conducted to describe age, growth, food habits, and spawning of a population in Virginia.

MATERIALS AND METHODS

Study Area

Field sampling was conducted on the North Fork Holston River, a fourth-order stream in the Ridge and Valley Province of southwestern Virginia. The study site was a 350 m section at River Mile 86.9 (36°55′N, 81°40′W), about 8 km upstream from Saltville, Smyth County. The river at this site averages 29 m wide and consists primarily of riffle habitat with cobble and boulder substrate. Water temperatures, recorded daily with a Ryan 30-day thermograph, ranged from 1°C in February to 29°C in July. Water quality characteristics, collected monthly and analyzed with a Hach DR-EL/1 field kit, are summarized in Table 1. Detailed water quality data for the North Fork Holston River were compiled by Poppe (1982). A total of 41 fish species occurs at the study site (Widlak 1982).

Fish Collections

Redline darters were collected twice monthly from May to August 1981, and monthly from September 1981 to May 1982. Sampling was done exclusively with a Coffelt BP-1 backpack electroshocking unit with direct current output, and dip nets. Waterscopes were used to facilitate sighting of darters during high water levels. All habitats were electrofished to obtain representative samples of redline darters, and an attempt was made to collect at least 10 darters on each sampling date. Seventeen to one-hundred twenty-six specimens were collected per sample during summer and fall sampling, but only three to seventeen were collected during the winter months because of high water levels or ice conditions. Specimens were placed on ice to reduce regurgitation of

Table 1. Water chemistry characteristics collected monthly at North Fork Holston River Mile 86.9, January 1981-March 1982.

Characteristic	Mean	Range	N
Hardness (mg/ l)	130	90-175	12
Alkalinity (mg/ l)	116	70-160	14
pH	7.1	6.6-8.3	12
Dissolved oxygen (mg/ l)	9	7-12	12
Turbidity (FTU)*	14	0-25	11
Conductivity (μ mhos)	143	81-218	12

* FTU = Formazin turbidity units

stomach contents before preservation in 10% buffered formalin. Preservation produced a mean shrinkage of 2 mm in length and gain of 0.2 g in weight. In the laboratory, the preserved fish (499 males, 183 females) were measured (total lengths to nearest 1.0 mm) and weighed (to nearest 0.1 g).

Age and Growth

Scale samples from 126 males and 65 females were taken from the left side above the lateral line and below the spiny dorsal fin at the tip of the depressed pectoral fin, mounted on optical plastic slides, and examined under a compound microscope at 10X magnification. Measurements were made with an ocular micrometer from the center of the focus to each annulus and to the scale margin in the anterolateral field. Length-frequency distributions were plotted as a check on scale readings. Age and growth data for males and females were analyzed using a computer program developed by Marques et al. (1982). Regressions for body length-scale radius relation were fitted by linear regression and length-weight relations were computed. Growth curves were fitted to the von Bertalanffy growth equation (Ricker 1975):

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where L_t = total length (mm) at time t, L_∞ = asymptotic length (mm), K = growth coefficient, t = time (age), and t_0 = hypothetical age at zero length. Annual survival of males and females was computed by the unbiased minimum variance estimator of Chapman and Robson, which is based on coded ages and the frequency of individuals in each age class (Everhart et al. 1975). Since age 0 and I fish were less vulnerable to the sampling gear, they were not included in these survival estimates.

Food Habits

Ten darters per month, sampled randomly from collections made during each sampling period, were dissected to determine seasonal food

habits. If fewer than 10 fish were collected in a month, all specimens were examined. Stomach contents were removed, sorted, identified to order or family (Hilsenhoff 1975; Merritt and Cummins 1978; Barnes 1980), and counted. Sampling to determine feeding chronology was conducted on 2 July, 13 August, and 9 September 1981. Twelve to twenty-four darters were collected during each of six 4-hour intervals (1200, 1600, 2000, 2400, 0400, and 0800). Stomach contents were pooled for each sampling time, blotted on a paper towel, and volumetric displacement was measured with a 1 cc plastic syringe. Mean stomach volume for each time interval was computed. These 24-hour samples (329 fish) were also included in seasonal food habits analyses.

Reproduction

The reproductive cycle of the male was studied by recording the size and appearance of testes of 427 males, and by external body coloration. Ovaries and digestive tracts of females were removed, and the ovaries weighed to the nearest 0.01 g. Adjusted body weights (body weight after removal of stomach, ovaries, intestinal tract, and liver) of females were also obtained. Ovaries were examined under a dissecting microscope and classified as (1) gravid - containing maturing eggs; (2) ripe - containing ripe eggs; (3) spent - containing some ripe eggs and showing apparent resorption; and (4) resting - containing no mature or maturing eggs. All eggs in both ovaries were counted and categorized as (1) mature (ripe) - largest in size, translucent, indented, and containing a single large oil globule; (2) maturing - intermediate in size, opaque, and yellow; and (3) immature - smallest in size, round, and white. Samples of 10 mature and maturing eggs from each pair of ovaries were measured to the nearest 0.1 mm with an ocular micrometer. A gonosomatic index (GSI) was calculated for females by multiplying the ovary weight by 1000 and dividing by the adjusted body weight (Burr and Page 1978, 1979); values were then plotted over time. No female darters were collected in January and only two in December; consequently, these months were not represented in the GSI computations. Analysis of covariance tested for homogeneity between ovary weight and body weight, total length, $\log_{10}$ body weight, and cube of total length (de Vlaming et al. 1982). Relations between ova diameter, number of mature and maturing ova, and total length of female, and ova number and adjusted body weight in pre-spawning fish were computed by simple linear regressions. Attempts to observe spawning at the study site and in the laboratory, and to rear darters for larval descriptions, were unsuccessful.

RESULTS AND DISCUSSION

The redline darter was the predominant darter and one of the most abundant fish species at the study site. A total of 682 was collected

during the study. Large males (longer than 50 mm) occurred consistently in the swiftest sections of riffles; smaller males and females were collected in swift riffles during summer, but were found frequently in areas with moderate current or along the margins of riffles in other seasons. Young-of-the-year darters were not well represented in samples, and were generally found in protected areas with low current velocity, adjacent to emergent vegetation or streamside brush. Larval darters apparently drift passively into pool areas (Scalet 1973) and have been found at depths of 3 meters (Stiles 1972). The habitat of redline darters in the North Fork Holston River concurs with that reported for other *Nothonotus* species (Raney and Lachner 1939; Raney and Suttkus 1964; Zorach 1969, 1970).

Age and Growth

Scale radius and total length of fish were strongly correlated ($r = 0.85$, females; $r = 0.93$, males). Regenerated scales were common on fish of all sizes, but at least three readable scales were available from each fish collected. Annuli were recognized by crowding of circuli in the anterior field and cutting over in the lateral field. Annulus formation was in early to mid-March at water temperatures of 5° to 20°C, as is typical of other darter species (Fahy 1954; O'Neil 1981; Shute et al. 1982). The body-scale relations for males and females were linear. Equations for the fitted regression lines were as follows:

$$\text{Males} \quad L = 14.3 + 0.619\,(S) \quad (R^2 = 0.859)$$
$$\text{Females} \quad L = 10.0 + 0.708\,(S) \quad (R^2 = 0.720)$$

where L = total length (mm) and S = scale radius magnified (focus to margin in the lateral field in mm). Back-calculated lengths, based on scale measurements, approximated actual lengths of darters at capture for all age classes (Table 2). Length-frequency distributions for males and females did not provide an adequate indication of age class structure. Scale readings were assumed to be accurate because a random sample of 30 scales was aged, with few discrepancies, by several fishery biologists. Young-of-the-year darters appeared as an identifiable age class in June, but overlap between lengths of 40 to 60 mm obscured separation of the intermediate age classes (I and II). Scale analysis indicated that maximum age for males and females was four years and three years, respectively. Chapman-Robson estimates for annual survival were 0.28 (±0.003) for males and 0.03 (±0.001) for females.

Growth of redline darters was rapid and uniform for all age classes. Because only one age III female (67 mm) was collected, length-at-age data were insufficient to obtain a reliable growth equation for females. The von Bertalanffy growth parameters for males were as follows:

$$L_\infty = 88 \text{ mm}, \; t_0 = -0.815 \text{ years}, \; K = 0.378$$

Table 2. Actual and back-calculated lengths (linear regression) at capture for redline darters, North Fork Holston River, May 1981-May 1982.

Sex and age	N	Actual length (mm)	Back-calculated (mm)
Males			
I	54	43.6	44.8
II	49	58.1	56.9
III	19	65.7	65.7
IV	4	76.7	75.6
Females			
I	34	41.9	43.0
II	30	54.7	53.3
III	1	67.0	65.2

Table 3. Numerical abundance and percent of total number of food items for different categories of food in 546 redline darter stomachs, 1981-1982.

	Dec-Feb (N=10)		Mar-May (N=36)		Jun-Aug* (N=377)		Sep-Nov (N=123)	
Food	No.	%	No.	%	No.	%	No.	%
Diptera								
Chironomidae	120	86.3	208	65.6	1665	59.8	855	62.9
Simuliidae	1	0.7	25	7.9	203	7.3	171	12.6
Other	-	-	5	1.6	36	1.3	11	0.8
Ephemeroptera								
Baetidae	5	3.6	19	6.0	212	7.6	75	5.5
Heptageniidae	1	0.7	8	2.5	118	4.2	25	1.8
Siphlonuridae	-	-	11	3.5	98	3.5	55	4.0
Other	1	0.7	7	2.2	4	0.1	5	0.4
Trichoptera								
Hydropsychidae	2	1.4	5	1.6	130	4.7	79	5.8
Hydroptilidae	6	4.3	6	1.9	130	4.7	14	1.0
Other	-	-	5	1.6	29	1.0	11	0.8
Plecoptera	-	-	-	-	5	0.1	-	-
Coleoptera	-	-	-	-	8	0.2	3	0.3
Hydracarina	3	2.2	16	5.1	122	4.4	56	4.1
Nematomorpha	-	-	2	0.6	-	-	-	-
Empty stomachs	1	10.0	2	5.6	37	9.8	14	11.4
Totals	139	100	317	100	2784	100	1360	100

* Crayfish, fish eggs, and unidentified invertebrate eggs were collected in a few stomachs during this period.

Males grew rapidly during the first two years of life and slowed thereafter. The largest male collected was 80 mm (age IV), approaching the estimated maximum length of 88 mm for males. Length-weight relations for male and female redline darters were described by the following regression equations:

$$\text{Males } \log_{10} W = -5.42 + 3.32 \log_{10} L \quad (R^2 = 0.987)$$
$$\text{Females } \log_{10} W = -5.11 + 3.14 \log_{10} L \quad (R^2 = 0.956)$$

where W = weight (g), and L = total length (mm). Both sexes grew at similar rates.

Food Habits

Contents of 546 stomachs were identified and tabulated (Table 3). Empty stomachs made up only 9.9% (range, 5.6 to 11.4%) of the total sample by season (Table 3). Dipteran larvae were the dominant food items throughout the year. Chironomidae and Simuliidae made up from 67.1% of the diet in June-August to 87.0% in December-February, and occurred in 10.0 to 83.3% of the stomachs examined monthly. Ephemeroptera and Trichoptera larvae were important items in summer and fall; 9.8 to 29.3% of stomachs examined from June to November contained these larvae. Hydracarina were eaten throughout the year, but were most common in stomachs in March to May (5.1% of the diet). Food of young-of-the-year was not determined, but may have been largely zooplankton, as reported for the young of other species (Scalet 1972; Burr and Page 1978, 1979; Page 1980). The food of juveniles 25 to 40 mm was similar to that of adults. Items found infrequently in stomachs (less than 1% of the diet) included Plecoptera, Coleoptera, Nematomorpha, and unidentifiable invertebrate eggs. Fish eggs and small crayfish (Decapoda) were found in the stomachs of several large males (60+ mm).

Sample sizes for the 24-hour feeding studies on 2 July, 13 August, and 9 September were 95, 126, and 98 fish, respectively. Stomach content analyses indicated a distinct feeding chronology and similar feeding patterns on all three sampling dates (Fig. 1). Mean food volumes in stomachs increased from mid-morning through late afternoon and early evening, and decreased from late evening to early morning. Feeding peaks were at 2000 hr on 2 July (0.021 ml/stomach) and 9 September (0.028 ml/stomach), and at 1600 hr on 13 August (0.027 ml/stomach). None of the fish collected at 1600 hr on the three dates had empty stomachs, but 18 to 30% of those collected at 2400 hr and 76 to 78% collected at 0400 hr were empty. These observations suggest that redline darters are diurnal sight feeders. Scalet (1972) reported that *Etheostoma radiosum* when feeding may rely on visual cues, particularly on movements of prey, and similar visual feeding has been proposed for other darter species (Mathur 1973; Adamson and Wissing 1977; Schenck and Whiteside 1977).

REPRODUCTION

Darters less than 35 mm long could not be sexed by external characteristics or by gonadal examination and were considered juveniles. Adult males and females were easily distinguished by their sexual dichromism. Males in breeding condition were readily distinguishable from non-breeding males by body coloration. Non-breeding males lacked coloration on fins and pelvic region and were similar in appearance to non-breeding females. Their testes were small and translucent. In contrast, the vertical fins of breeding males were edged with a band of dark green and inner bands of white and bright red. The basal portion of these fins was dusky gray. Paired fins were yellow or greenish-yellow basally and edged with bright red. The pelvic region was dark green and the abdomen creamy white to yellow. Body coloration varied from light tan to dark brown, with bright red lateral spots. Testes were enlarged, creamy white, and opaque. Bright coloration was apparent on males throughout the year, but enlargement of testes was not observed until March. Males in spawning condition were collected throughout spring and summer, but testes were reduced in size in all fish collected in September. About 72% of age I males, all those longer than 40 mm, were sexually mature.

Females were less colorful although breeding females were generally darker than others. They lacked the bright coloration on the fins and body; vertical and paired fins were heavily spotted with black. The body was darker than that of the male and lacked red spots, but the caudal base of both sexes had prominent white spots. All females collected between September and mid-February had resting ovaries, and ova development first became apparent in March. By May the ovaries contained both maturing and fully ripe ova. Females also reached sexual maturity at age I; 56% of age I females were in spawning condition. The smallest ripe female (42 mm long) was collected in July 1981.

Sex ratios of redline darters at the study site were strongly skewed in favor of males. The overall ratio of males to females was 2.7:1, a significant deviation from a 1:1 sex ratio ($\chi^2 = 146.4$, $p < 0.005$). Seasonal differences or sampling biases may have contributed to the apparent temporal changes in distribution of the sexes. During summer, the sex ratio averaged 2.5:1, since both sexes were present in riffles for spawning. As females moved out of shallow riffle areas after spawning, the sex ratio increased to 5:1 (September) and then returned to 2.5:1 as age 0 individuals were recruited into the population. It is likely that electrofishing was selective for males. Darters shocked in swift riffles were swept into the water column and easily netted, while those in other areas often remained on the bottom and were more difficult to collect.

Total egg complements of 85 female redline darters ranged from 50

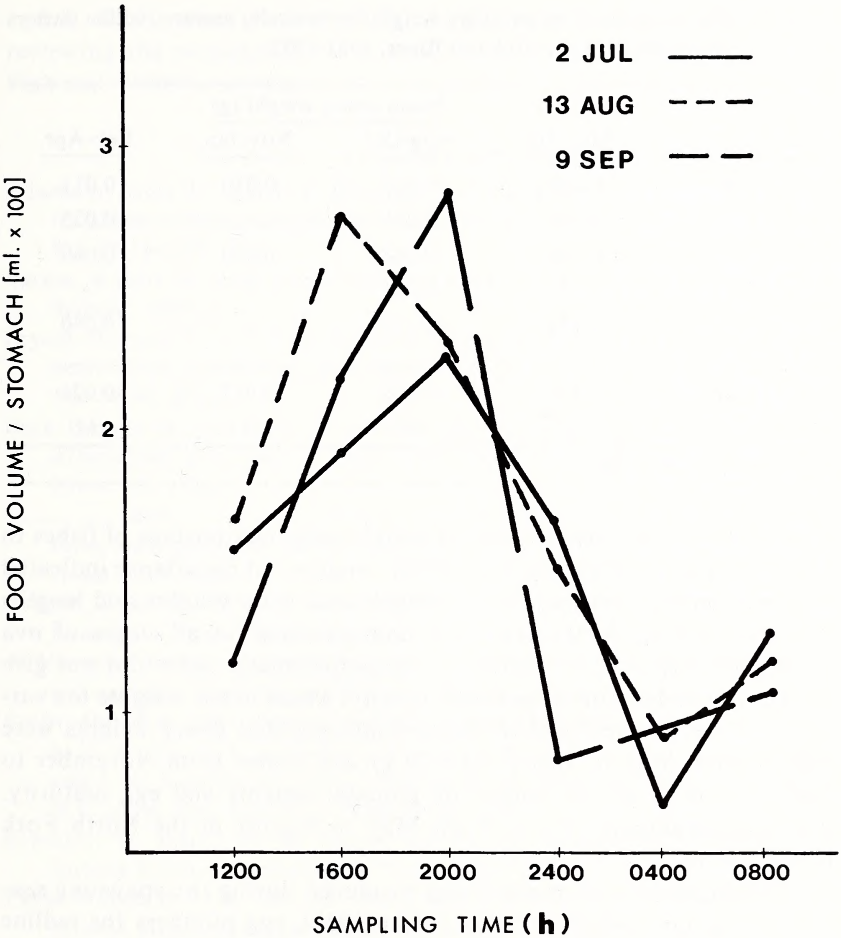

Fig. 1. Twenty-four hour feeding chronologies for redline darters in the North Fork Holston River, 2 July, 13 August, and 9 September 1981.

to 331; numbers of maturing (diameter 0.7-1.5 mm) and mature (1.6-2.2 mm) eggs combined ranged from 23 to 131. Diameter of mature ova and total length of female were not significantly correlated (r = 0.08). The number of mature ova and total length of female, and the number of mature ova and adjusted body weight, were slightly correlated (r = 0.498 and 0.537, respectively).

Spawning occurred between May and August 1981 at water temperatures of 14° and 26°C. Ripe females were collected as early as 3 May and as late as 18 August. The gonosomatic index (GSI) was not used to identify the spawning season of redline darters because previous

Table 4. Comparison of mean ovary weights of sexually mature redline darters in the North Fork Holston River, 1981-1982.

	Mean ovary weight (g)			
Size class (mm)	May-Jul	Aug-Oct	Nov-Jan	Feb-Apr
40-44	0.054	0.012	0.010	0.011
45-49	0.086	0.031	-	0.035
50-54	0.146	0.048	0.020	0.060
55-59	0.145	0.061	-	-
60+	0.174	0.110	-	0.080
Mean	0.118*	0.042	0.017	0.026
N	62	85	3	11

*Significant at $p = 0.05$.

statistical analyses have shown the ovary-body relationships of fishes to be misleading (de Vlaming et al. 1982). Analysis of covariance indicated that relationships between ovary weights and body weights and lengths in female redline darters were not homogeneous for all stages of ova development ($p<0.001$); therefore, the gonosomatic index did not give an accurate indication of gonadal activity. Mean ovary weights for various size classes presented in Table 4 indicate that ovary weights were highest from May to July (0.01-0.29 g) and lowest from November to April (0.01-0.08 g). As judged by gonadal weights and egg maturity, spawning apparently occurs from May to August in the North Fork Holston River.

Assuming that all mature eggs produced during the spawning season by a gravid female are laid (Winn 1958), egg numbers for redline darters in this study (23 to 131) are lower than those reported for other darter species (Winn 1958; Bryant 1979; Burr and Page 1979; Lindquist et al. 1981). Winn (1958) reported that in several species females spawn with different males and lay only a few eggs at each spawning. Female redline darters have been observed burying themselves in the gravel several times during spawning, laying several eggs at a time (Stiles 1972). Females may already have laid a portion of their eggs before collection in summer, and egg numbers reported here may not represent total numbers of eggs laid during the spawning season. The unusually low correlation between total length of females and number of eggs tends to support that conclusion.

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Rete Mirabile Ophthalmicum and Intercarotid Anastomosis in Procellariiformes Taken off the North Carolina Coast

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ABSTRACT.— Dissections of arterial circulation patterns were made in eleven species of procellariiform birds taken off the coast of North Carolina. All species possessed well-developed rete mirabile ophthalmicums (RMO) and intercarotid anastomoses, both playing a role in selectively shunting blood flow and counter-current heat exchange to facilitate thermoregulation and maintaining brain temperatures lower than body temperatures during heat stress. There was no correlation between relative size of the RMO and nesting latitude, but RMO size was relatively greater in the smaller members of the order.

INTRODUCTION

Kilgore et al. (1979) and Bernstein et al. (1979a, 1979b) showed that the presence of a rete mirabile ophthalmicum (RMO) was associated with a reduction in brain temperature in heat stressed birds. The rete facilitates counter-current heat exchange between the arterial blood supply to the brain and the venous blood draining the evaporative surfaces of the mouth and the cornea. RMO's have been reported in a number of species (Richards and Sykes 1967; Lucas 1970; Kilgore et al. 1976; Crowe and Crowe 1979; Pettit et al. 1981). Pettit et al. (1981) examined the anatomy of the RMO of Hawaiian seabirds that may encounter stressful thermal environments at their tropical nesting sites. An additional site for possible counter-current heat exchange lies in the cavernous sinus that houses the carotid vein and the intercarotid anastomosis (Baumel and Gerchman 1968). These authors described three major types of intercarotid anastomoses in birds.

My study was undertaken to determine if the RMO and the type of intercarotid anastomosis in procellariiform birds breeding near the poles, in the temperate zones, and in the tropics differed, perhaps in response to thermal stresses encountered at the nesting colony. One might predict that tropical, open, ground-nesting species are exposed to greater thermal stress and therefore would have relatively larger retes.

METHODS

Most specimens were collected 30 to 60 km off the North Carolina

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coast, but a few specimens of the Northern Fulmar, *Fulmarus glacialis*, and the Sooty Shearwater, *Puffinus griseus*, were found dead on North Carolina beaches. The lone Antarctic Petrel, *Thalassoica antarctica*, was obtained from D. G. Ainley via D. W. Johnston in trade. All specimens on which this note is based are deposited in the collection of the North Carolina State Museum of Natural History. Dissections under a binocular microscope were in most cases performed on pickled specimens, using the methodology of Pettit et al. (1981).

RESULTS

Two of the three types of intercarotid anastomoses were found in the eleven procellariiform species examined in this study (Table 1). There was no correlation of anastomosis type with latitude (as an index of potential thermoregulatory stress).

In all cases the RMO was found in the temporal region of the head, between the orbital ridge and the otic process of the quadrate. The RMO is derived from the external ophthalmic branch of the internal carotid artery and from branches of the facial, maxillary and mandibular veins. To crudely assess the relative size of the rete in 11 species of Procellariiformes ranging in weight from 34 to 774 grams, I measured the surface area of the RMO using a transparent grid. This measure does not take into account the relative thickness or, more importantly, the actual area of contact of the arterial and venous components of the rete. However, it does give a first approximation of the relative size of the rete. Surface area/body weight ratios exhibited a slight but insignificant ($P>0.05$) increase with latitude (Table 2), while an inverse correlation ($P<0.05$) of body weight and RMO surface area/weight ratio was evident. Thus, the smaller procellariiforms have relatively larger RMO's.

DISCUSSION

A well-developed intercarotid anastomosis unites the two carotids caudal to the hypophysis in most birds examined by Baumel and Gerchman (1968). They found that injection of the cervical portion of one carotid resulted in bilateral filling of both the intra- and extracranial arteries via this anastomosis. The avian intercarotid anastomosis may effectively substitute for the mammalian circle of Willis in maintaining brain-to-body temperature differences (Baumel and Gerchman 1968; Kilgore et al. 1976; Pettit et al. 1981).

As Kilgore et al. (1976) pointed out, the effectiveness of the RMO heat exchange depends on the arterial-venous temperature differential, on rete blood flow and velocity, and the area and closeness of arterial-venous contacts within the rete.

Several species, including Sooty and Greater Shearwaters, and Wilson's Storm-Petrel, *Oceanites oceanicus*, are transequatorial migrants

Table 1. Pattern of intercarotid anastomosis in 46 specimens of 11 species of Procellariiformes. N = number examined.

Species	N	Pattern of anastomosis[1]			Latitude of breeding range[2]
		X	X-H	H	
Fulmarus glacialis	2	2			50-85° N
Thalassoica antarctica	1	1			72-76° S
Pterodroma hasitata	4	4			14-20° N
Calonectris diomedea	13	13			14-40° N
Puffinus gravis	4	4			36-40° S
Puffinus griseus	3	3			52-56° S
Puffinus puffinus	2	2			28-65° N
Puffinus lherminieri	7	7			10-33° N
Oceanites oceanicus	8	4	3	1	51-75° S
Oceanodroma leucorhoa	1	1			42-64° N
Oceanodroma castro	1	1			30-40° N

[1]X-type is defined as having cerebral carotids anastomosing side-to-side, H-type has a pronounced transverse anastomosis joining the two carotids, and X-H type is intermediate with a short transverse anastomosis (after Baumel and Gerchman 1968).

[2]from Palmer (1962) or Watson (1975).

that may be exposed to thermal stress while flying across the doldrums (equatorial zone with little wind). Their retes are not appreciably larger than those of north or south temperate zones or Antarctic species. Birds collected while they were flying at sea off North Carolina did not exhibit elevated body temperatures (Platania et al., in press). The RMO of the Black-capped Petrel, *Pterodroma hasitata*, a tropical species, is not different from that of other species of higher latitudes. The bird is not subjected to heat stress at its nesting grounds because it is a winter (Northern Hemisphere) breeder, and because at high elevations it excavates burrows. Altitude, and the extent of the use of burrows for nesting, further cloud simple correlations of RMO ratios with latitude. In general, the smaller birds nest exclusively in burrows or crevices while the larger shearwaters and fulmars are open ground or cliff nesters. In addition, most ground-level activity of burrowing species occurs at night, further reducing heat stress.

As arterial blood may reach the brain via several routes (Richards and Sykes 1967; Richards 1970; Crowe and Crowe 1979), involving both direct and indirect (via extensive anastomoses) flow, the potential exists for selectively regulating flow under varying conditions. Flow of arterial blood may be shunted through the RMO to the brain via anterior anastomoses with intracranial branches of the internal carotid. This could

Table 2. Surface area of rete and body weight ratios of 11 species of Atlantic Procellariiformes. Data presented as mean ± 1 standard deviation (sample size).

Species	Rete surface area (mm^2)	Weight of birds (g)	Surface area/ weight (mm^2/g)	Average breeding latitude
Northern Fulmar *Fulmarus glacialis*	35.10±0.92(2)	692.3±78.5(20)[a]	0.05	67° N
Antarctic Petrel *Thalassoica antarctica*	28.60(1)	639[b]	0.04	74° S
Black-capped Petrel *Pterodroma hasitata*	32.11±6.21(5)	431.1±47.1(5)	0.07±0.01(5)	17° N
Cory's Shearwater *Calonectris diomedea*	31.45±3.18(13)	568.8±80.6(12)	0.06±0.01(12)	27° N
Greater Shearwater *Puffinus gravis*	36.08±1.50(4)	626.6±29.9(3)	0.06±0.01(3)	38° S
Sooty Shearwater *Puffinus griseus*	36.18±1.35(3)	774.0(1)[a]	0.04	54° S
Manx Shearwater *Puffinus puffinus*	26.00±1.84(2)	359.2±34.0(2)	0.07±0.01(2)	47° N
Audubon's Shearwater *Puffinus lherminieri*	14.67±1.98(7)	179.8± 4.4(6)	0.08±0.01(6)	22° N
Wilson's Storm-Petrel *Oceanites oceanicus*	3.49±0.77(8)	34.3± 2.9(6)	0.10±0.02(6)	63° S
Leach's Storm-Petrel *Oceanodroma leucorhoa*	3.90(1)	40.8(1)	0.10(1)	53° N
Band-rumped Storm-Petrel *Oceanodroma castro*	4.55(1)	48.4(1)	0.09(1)	35° N

[a]from Platania et al. (in press)
[b]mean of values in Brown et al. 1982

serve to maintain brain temperatures lower than core body temperatures during heat stress (Kilgore et al. 1979; Bernstein et al. 1979a, b). During cold stress the arterial blood flowing to the anterior surface of the head is cooled by returning venous blood in the RMO (Frost et al. 1975). Undue loss of body heat is prevented in the RMO by counter-current heat exchange. In this example, the anastomoses with the intracranial arteries are not open; blood flow to the brain is achieved directly via the internal carotid. Therefore, the lack of correlation between size of RMO and latitude (as an indicator of temperature stress) may indicate that the RMO functions during both cold and heat stress. The relatively larger RMO in smaller birds is probably related to their relatively larger surface/volume ratios, and the relatively greater stress they encounter as environmental temperatures fluctuate.

In summary, all 11 species of procellariiform birds examined possessed a rete mirabile ophthalmicum. There was no correlation between relative size of RMO and nesting latitude, but RMO size was relatively greater in the smaller members of the order.

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Notes on *Virginia* (Reptilia: Colubridae) in Virginia

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ABSTRACT.— Female *Virginia striatula* in central Virginia produce an average of 6.0 young/litter and reproduce annually. Litter size, frequency of reproduction, oviductal egg size and size of newborn young are greater than those of *V. striatula* from the southwestern part of its range in Texas. Absence of size classes below those of mature snakes suggests high mortality of subadults or perhaps sampling bias caused by behavioral differences between adults and young. Ventral and subcaudal counts of *V. striatula* from Virginia are low; comparison of these with the few measurements from the rest of the range indicates there is significant geographic variation, although the pattern is not clear. Data from *Virginia v. valeriae* collected in the same area are also provided.

INTRODUCTION

The genus *Virginia* includes two species of small, secretive, ground-dwelling snakes: the Rough Earth Snake, *Virginia striatula* (Linnaeus), and the Smooth Earth Snake, *Virginia valeriae* (Baird and Girard). In Virginia, *V. valeriae* is represented by the nominate subspecies, *V. v. valeriae*, the Eastern Earth Snake. Both species of *Virginia* are found throughout much of the southern tier of states from eastern Texas and Oklahoma to the Atlantic Coast (Conant 1975). The Rough Earth Snake reaches the northern edge of its known distribution along the Atlantic Coast in central Virginia. The Eastern Earth Snake occupies most of Virginia, and its distribution extends northward to New Jersey and Pennsylvania.

Few papers containing quantitative data have been published regarding *V. striatula* (Clark 1964; Clark and Fleet 1976), and nothing has been reported regarding the species in Virginia. As part of a long-term study of reptiles at the northern edge of their range, we report here morphometric and reproductive data for a population of *V. striatula* in central Virginia. The collecting location is near the apparent northern extreme of the species' range (Conant 1975; Martof et al. 1980). Additionally, we provide information about a smaller sample of *V. v. valeriae* collected in the same area.

MATERIALS AND METHODS

Data were taken from freshly collected specimens and preserved material in the Virginia Commonwealth University herpetological collection. Twenty-six male and forty-six female *V. striatula* are included. Four of the females lacked tail tips, so sample sizes of subcaudal counts and tail lengths are reduced accordingly. Thirteen male and seventeen female *V. valeriae* are also included. Most specimens were collected in eastern Henrico County, about 16 km east of Richmond. Two *V. striatula* and three *V. valeriae* were obtained from sites in Chesterfield County, approximately 20 km south of the Henrico locality. Snakes were collected in the period 1974-1980, but 85% of the sample was obtained during 1978-1980. The Henrico site is covered by a secondary growth of loblolly pine, *Pinus taeda*, within which are piles of roofing, discarded furniture, and tires. Besides *Virginia*, 14 other species of reptiles have been collected at the site, including one turtle, *Terrapene carolina*; five lizards, *Sceloporus undulatus hyacinthinus*, *Scincella lateralis*, *Cnemidophorus sexlineatus*, *Eumeces fasciatus* and *Eumeces inexpectatus*; and eight other snakes, *Storeria occipitomaculata*, *Storeria dekayi*, *Carphophis amoenus*, *Diadophis punctatus*, *Heterodon platyrhinos*, *Coluber constrictor*, *Elaphe obsoleta*, and *Agkistrodon contortrix mokasen*. *Virginia striatula* is the most common reptile at this locality.

Snout-vent and tail lengths were measured to the nearest millimeter. Ventral and subcaudal scales were counted in standard fashion (e.g. see Schmidt and Davis 1941) and the style is comparable to that used by Clark and Fleet (1976). Sex, number of ova/embryos, and stomach contents were determined by dissection. Testes and ova lengths were measured to the nearest millimeter. Embryos were removed and examined microscopically to determine extent of development. Developmental stages were assigned according to criteria in Zehr (1962). The 5% level of significance ($P<0.05$) was used in all statistical tests.

RESULTS

Morphometrics

There is no statistical intersexual difference in snout-vent lengths of *V. striatula* ($t = 1.5$, $df = 70$; Table 1), but significant differences exist between tail lengths ($t = 2.6$, $df = 63$), tail length/snout-vent length ratios ($t = 6.9$), ventral scale counts ($t = 2.6$) and subcaudal counts ($t = 9.3$). There also is no statistical difference between snout-vent length of sexes of *V. valeriae* ($t = 0.7$, $df = 28$; Table 2). However, statistical differences do exist between tail lengths ($t = 3.0$, $df = 28$), tail length/snout-vent length ratios ($t = 10.1$), ventral scale counts ($t = 5.7$) and subcaudals ($t = 13.3$).

Table 1. Comparison of *Virginia striatula* from Virginia and Brazos County, Texas. All values are means ± one standard error; sample sizes are in parentheses. All lengths are in mm; SVL = snout-vent length.

Measurement	Present study	Clark (1964)
Litter size	6.0 ± 0.3 (24)	4.9 ± 0.5 (16)[a]
SVL; males	164.2 ± 6.6 (26)	148.0 ± 2.5 (169)
SVL; gravid females	210.1 ± 3.9 (24)	226.0 (16)[b]
SVL; all females	179.7 ± 7.6 (46)	167.2 ± 3.6 (155)
Tail length; males	41.5 ± 1.8 (26)	20.6 ± 0.1 (133)
Tail length; females	35.0 ± 1.5 (42)	16.9 ± 0.1 (126)
Tail length/SVL; males	0.253 ± 0.004 (26)	-
Tail length/SVL; females	0.203 ± 0.002 (42)	-
Ventrals; males	118.7 ± 0.3 (26)	126.2 ± 0.2 (169)
Ventrals; females	125.2 ± 0.3 (46)	133.2 ± 0.2 (155)
Subcaudals; males	42.4 ± 0.6 (26)	46.6 ± 0.2 (133)
Subcaudals; females	36.2 ± 0.2 (42)	39.3 ± 0.2 (125)

[a] Litter size in Clark and Fleet (1976) is 5.3 ± 0.5 (12)

[b] SVL in Clark and Fleet (1976) is 218.0 (12)

Table 2. Morphometric data for *Virginia valeriae* in central Virginia. Values are means ± one standard error. See text for sample sizes.

Measurement	Males	Females
Snout-vent length (mm)	135.1 ± 8.5	145.4 ± 12.5
Tail length (mm)	30.6 ± 2.2	22.5 ± 1.6
Tail length/snout-vent length	0.225 ± 0.004	0.160 ± 0.005
Ventrals	114.6 ± 0.5	119.5 ± 0.7
Subcaudals	35.4 ± 0.5	26.0 ± 0.5

Sex Ratios and Reproduction

Significantly more female *V. striatula* were collected than males ($\chi^2 = 5.0$, Yates continuity correction performed). We found no significant difference in sex ratios of *V. valeriae*.

The smallest gravid *V. striatula* was 175 mm snout-vent length. Thirty-one of the forty-six females (67%) in this study reached or exceeded this size, and mean size of mature females was 210.0 mm (SE = 3.9). Excluding those females below 175 mm and those mature females captured outside the reproductive period (see below), 100% (24/24) possessed yolked eggs and/or embryos or gave birth to young in the laboratory. Size of ovarian eggs apparently begins to increase in late

March or early April, and ovulation occurs by mid to late May (Fig. 1, Table 3). Birth probably occurs in late July or early August. One female bore young in the lab on 10 August. Mean litter size, as based on the number of fertilized or yolked eggs or young, was 6.0 (range 4-10, N = 24).

The smallest gravid *V. valeriae* was 185 mm snout-vent length. Only 6 of the 17 females in this study reached or exceeded this size. Of these, 83% (5/6) possessed enlarged ova or embryos. Mean litter size is 6.6 ± 0.8 (N = 5). Ovarian eggs appear to increase in size at about the same time as those of *V. striatula*, and one female bore four young in the laboratory on 3 August.

Developmental stages (Table 3) of gravid female *V. striatula* seemed to conform closely to Zehr's (1962) scheme. In some females there was a small amount of variation in degree of development of embryos, but never more than three stages were present. Although Zehr recognized 37 stages, in practice the first 5 stages (pre-blastodisc) are difficult to recognize. Later stages can be recognized with some precision, and in our material, development of embryos confirms the timing of reproduction described above.

Most of the male *V. striatula* collected in our study were sexually mature as concluded from convolution of the vasa deferentia and enlargement of the testes. Clark (1964) found that minimum body length of mature males was 142 mm; 69.2% (18/26) of our sample exceeded 164 mm (none in the size interval 138-163 mm were collected), and all had convoluted vasa deferentia. Right testes length in mature *V. striatula* ranged from 5 to 12 mm. No seasonal cycle in testes size could be demonstrated as the length of testes varies with snout-vent length, obscuring temporal variations. At least 53.8% (7/13) of the male *V. valeriae* were over 125 mm and appeared to be sexually mature. These had enlarged testes (6-12 mm) and also had convoluted vasa deferentia.

Food

Only 19.6% (20/102; 12 *V. striatula*, 8 *V. valeriae*) of the *Virginia* collected in this study contained food. All recognizable items consisted of small pieces of red annelids that we were not able to identify further.

DISCUSSION

Clark (1964) published an analysis of an extensive series (324 specimens) of *V. striatula* collected in Brazos County, Texas, and Clark and Fleet (1976) provided ecological data for a population in the same area. Both sites are near the southwestern edge of the species' range (see Conant 1975). Snout-vent lengths and tail lengths of the males in Clark's study differed significantly from those in our study (t = 2.3 and

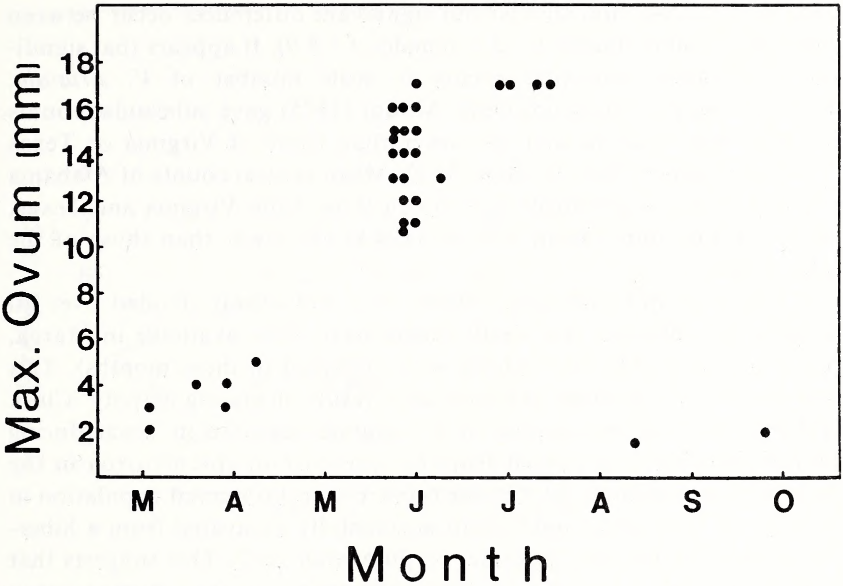

Fig. 1. Seasonal variation in maximum size of ova or ovarian follicles of mature female *Virginia striatula* from Virginia.

Table 3. Stage of development of eggs of the rough earth snake, *Virginia striatula*.

Date	Number of broods	Number of eggs/young	Stage
24 May 1980	5	5,5,6,6,8	<6 to 7
27 May 1980	7	4,5,5,6,6,7,7	yolked ova to 14
31 May 1980	6	4,5,6,7,7,10	<6 to 20
7 June 1976	1	8	26
25 June 1980	1	4	27-28
29 June 1980	1	5	29
7 July 1980	1	9	31-32
9 July 1980	1	4	28-29
10 August 1980	1	7	birth

2.4; df = 193, 157), while those of females did not (t = 1.3 and 1.3; df = 199, 170). There was no significant difference in tail length/snout-vent length ratios (males: t = 1.3; females: t = 0.4). In both our data and those of Clark and of Clark and Fleet, shrinkage corrections were made after the specimens were preserved. Scale counts of Virginia specimens are lower than those of Texas material. Ventral counts differ greatly (males: t = 20.8;

females: $t = 22.4$). and smaller but significant differences occur between subcaudal counts (males: $t = 2.3$; females: $t = 8.9$). It appears that significant geographic variation occurs in scale number of *V. striatula*, although the pattern is not clear. Mount (1975) gave subcaudal counts for Alabama *striatula* that are lower than those of Virginia or Texas specimens (males: 38.5; females: 34.2). Mean ventral counts of Alabama males (121.2) are intermediate between those from Virginia and Texas, while ventral counts from females (124.8) are lower than those of the other states.

Although our collecting efforts were not evenly divided over all months, it is obvious that earth snakes were more available in March, April and May (63/102 = 61.8% were collected in these months). This may be due to increased exposure as a result of mating activity. Clark (1964) concluded that mating of *V. striatula* occurred in Texas during March and April, as judged from the presence of spermatozoa in the lumina of the oviducts. D. Greene (pers. comm.) observed copulation in a group of 30 or more individuals accidentally excavated from a hibernaculum at Richmond, Virginia, on 30 March 1982. This suggests that first mating may occur shortly after emergence from the hibernaculae in early spring.

Size distribution of *V. striatula* in central Virginia seems skewed toward larger snakes. For example, males of *striatula* as small as 123 mm snout-vent length were collected in May, yet only 28.0% (7.25; newborn young excluded) of the entire sample was less than 164 mm (minimum size at maturity). For females, 123 mm also was a minimum size of May specimens, yet only 33.0% did not exceed 175 mm. This bias toward large size indicates either that subadult earth snakes are difficult to find, or that mortality rates of young are relatively great. We believe that the latter hypothesis is correct. Subadult snakes do not seem to behave differently from older snakes, as they often were found with adults or in similar sites. Also, the abundance of small *V. valeriae* supports this contention. About 41.7% (5/12; newborns excluded) of male *V. valeriae* and 57.1% (8/14) of female *valeriae* were shorter than mature individuals. *Virginia valeriae* is not at the northern edge of its range as is *V. striatula* at this collection site. We hypothesize that midwinter mortality of young snakes may be important, as it is in the eastern cottonmouths, *Agkistrodon p. piscivorus* that also reach the northern edge of their range in this area (Blem 1981).

Gravid female *V. striatula* near the northern edge of the range are smaller than those reported by Clark (1964) and by Clark and Fleet (1976) in Texas (Table 1). Since error terms are not available for the Texas sample, statistical comparison is not possible. Clark and Fleet demonstrated a significant regression of litter size on snout-vent length

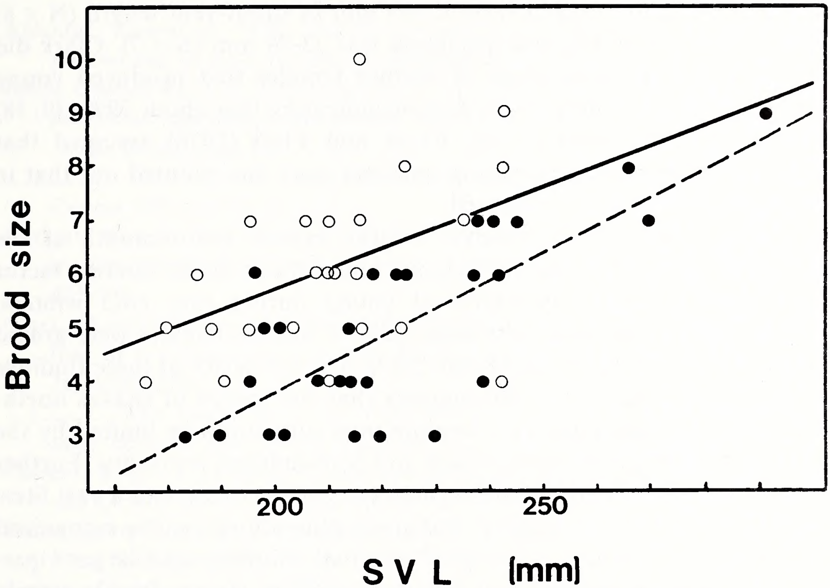

Fig. 2. Brood size as a function of snout-vent length (SVL, mm) in female *Virginia striatula*. Solid circles represent Texas specimens (Clark and Fleet 1976); hollow circles represent Virginia specimens. The dash line is the least-squares best-fit line for Texas snakes (brood size = 0.052 SVL - 6.647, r = 0.77); the solid line is the best-fit line for Virginia snakes (brood size = 0.038 SVL - 1.993, r = 0.46).

in which larger females produce larger numbers of ova or young. Statistical comparison of their data with ours demonstrates a significant interlocality difference (F = 20.4); slopes and intercepts of equations predicting brood size from female snout-vent lengths are significantly different (see Fig. 2). This means that female *V. striatula* in Virginia produce more eggs per reproductive attempt than do Texas females of similar size. Absolute brood size, as judged from numbers of fertilized ova or young per female, is significantly higher in Virginia females (t = 2.1; df = 38) than the values given by both Clark and Clark and Fleet, but the difference is not statistically significant in the latter comparison.

Further reproductive adjustment may occur through increased ova size. Clark (1964) found that the largest right ovarian follicle was larger than 5 mm only twice in a sample that included over 100 females (many of them over 180 mm snout-vent length), and concluded that one of these was abnormal. In our study, largest right ovarian follicles reached 12 mm and oviductal eggs were 12-17 mm long. Also, while 100% (24/24) of our females were gravid during the reproductive period, not all mature Texas females were. It may be significant that newborn

Texas *V. striatula* ranged from 61-69 mm in snout-vent length (N = 8) while the range of Virginia specimens was 73-79 mm (N = 7). Clark did not calculate the percentage of mature females that produced young each year, but we interpret his data as indicating that about 79% (30/38) should have produced young. Clark and Fleet (1976) assumed that mature females produced young once per year, but pointed out that in some years this was not achieved.

Blem (1981), in an analysis of the eastern cottonmouth at the northern edge of its range in Virginia, found that a major limiting factor was high overwinter mortality of young during very cold winters. Reproductive rates were very high; 83% of mature females were gravid during the breeding season (Blem 1982). The similarity of these findings to those of the present study suggests that the spread of snakes northward on the coastal plain of Virginia may sometimes be limited by the balance between reproductive rate and cold-induced mortality. Further comparison of our studies of *Virginia* and *Agkistrodon*, and a vast literature (e.g. Fitch 1970), suggest that some generalities may be recognized regarding reproductive "strategies" of small colubrids and larger viperids. In general, it appears that less than 100% of mature female viperid snakes reproduce each year and the proportion is often nearer 50% (Aldridge 1979; but see Kofron 1979 and Blem 1982 for exceptions). Conversely, 90-100% of the females of many colubrid species, particularly small snakes such as *Carphophis amoenus*, *Diadophis punctatus* and *Thamnophis sirtalis*, reproduce annually (Aldridge 1979). It therefore appears that one might expect a large proportion of the females of a population of *V. striatula* to be involved in the production of young each year. In many studies addressing reproductive output of snakes, a relationship has been noted between litter size, or some other measure of reproductive output, and female size (see Blem 1981, 1982). Both small colubrids (e.g. Clark 1964) and viperids show this phenomenon. However, frequency of reproduction appears to be a size-related phenomenon in some viperids (Burkett 1966; Blem 1982), while that relationship has not been demonstrated for small colubrids.

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THE SEASIDE SPARROW, ITS BIOLOGY AND MANAGEMENT

Edited by

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The proceedings of a symposium held at Raleigh, North Carolina, in October 1981, this book presents the keynote address of F. Eugene Hester, Deputy Director of the U. S. Fish and Wildlife Service, a bibliography of publications on the Seaside Sparrow, and 16 major papers on the species. Authors include Arthur W. Cooper, Oliver L. Austin, Jr., Herbert W. Kale II, William Post, Harold W. Werner, Glen E. Woolfenden, Mary Victoria McDonald, Jon S. Greenlaw, Michael F. Delany, James A. Mosher, Thomas L. Merriam, James A. Kushlan, Oron L. Bass, Jr., Dale L. Taylor, Thomas A. Webber, and George F. Gee. A full-color frontispiece by John Henry Dick illustrates the nine races of the Seaside Sparrow, and a recording prepared by J. W. Hardy supplements two papers on vocalizations.

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Fossil Bats (Mammalia: Chiroptera) from the Late Pleistocene and Holocene Vero Fauna, Indian River County, Florida

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ABSTRACT.— Six species of bats are reported from the late Pleistocene and Holocene Vero fossil vertebrate locality on the east coast of peninsular Florida: *Eptesicus fuscus*, *Lasiurus intermedius*, *L.* cf. *seminolus*, *Nycticeius humeralis*, *Tadarida brasiliensis*, and *Eumops glaucinus*. This is the first known fossil occurrence of *Lasiurus seminolus*, and the first record of *Nycticeius humeralis* from the Pleistocene of Florida. Previous reports of *Myotis austroriparius* from Vero are shown to be in error, as they were based on a misidentified humerus. The bats from Vero represent the most diverse fossil chiropteran fauna yet known from Florida and one of the richest in the North American Quaternary. This site is unique among Florida fossil vertebrate localities as it samples species of bats that roost primarily in trees, rather than cave-dwelling forms. The six species present at Vero constitute the entire native chiropteran fauna of present-day South Florida, indicating that the bat fauna of this region has remained relatively stable over the past 10,000 years.

INTRODUCTION

Recent curation of the abundant microvertebrate fossils collected by Robert D. Weigel in 1956 and 1957, during his re-excavation of the classic Vero Site on the Atlantic coast of Florida (Weigel 1962), revealed the presence of a relatively large sample of bat remains. Based on only four elements, Weigel (1962) recognized three genera of bats from Vero—*Myotis*, *Eptesicus*, and *Lasiurus*. He did not assign any of his material to species, and his identification of *Myotis* was incorrect. Detailed study of the bat fossils from Vero, especially the postcranial elements, and a re-examination of the small sample identified by Weigel, allows for more precise identification of most of the material. In the present study, six species of bats are recognized from the Vero deposits based on 37 elements representing 16 individuals. Comparison with data in Webb (1974:14, Table 2.1) indicates that the six species of bats at Vero make it the most diverse fossil bat fauna yet known from Florida.

DESCRIPTION OF LOCALITY

The Vero fauna is one of the best known late Pleistocene (Rancholabrean) local faunas in Florida (see Weigel 1962 for a complete list of

fossil vertebrates from Vero). Vero engendered considerable controversy in the early part of this century, as it was the first fossil site in the New World where human bones and artifacts were supposedly found in association with extinct Pleistocene vertebrates. The site was discovered in November 1913 during excavation of an east-west drainage canal through the town of Vero Beach by the Indian River Farms Company. Between 1913 and 1917, Isaac M. Weills and Frank Ayers collected the majority of the vertebrate fossils and human remains that formed the basis for a large number of publications on the site (see Ray 1957 and Weigel 1962 for a complete bibliography). The fossil site is located within the present city limits of Vero Beach, Indian River County, Florida (center of SE1/4, sec. 35, T32S, R39E, Vero Beach Quadrangle, USGS 7.5 min. series; 27°39'N latitude, 80°24'W longitude), southeast of the Vero Beach airport and immediately south of the Florida East Coast Railroad. The paleontological and historical significance of Vero, coupled with the paucity of microvertebrate fossils in the early collections, prompted Weigel to conduct extensive field work at the site during the summers of 1956 and 1957.

The fossil-bearing deposits at Vero consist of three distinct units, designated from bottom to top as Strata 1, 2, and 3 by Sellards (1917) and all later workers except Weigel (1962). He called them Beds 1, 2, and 3. According to Weigel, the three strata are easily recognized throughout the site and fill a shallow sedimentary basin approximately 100 m in diameter. A typical stratigraphic section at Vero and a map of his various excavations within the site can be found in Weigel (1962). The total thickness of strata at Vero does not exceed 3 m, of which only 1.5 to 2 m constitute the bone-bearing Strata 2 and 3. Stratum 1 is a late Pleistocene marine shell marl referred to the Anastasia Formation by Sellards (1916) that has produced no terrestrial or freshwater vertebrate fossils. Lying above the Anastasia Formation and separated from it by an erosional unconformity is Statum 2, consisting of white beach sands at the base, grading upward into coarse and fine brown stained sands that become darker toward the top of the bed. The vertebrate fossils from Stratum 2 are heavily permineralized and include 17 species of extinct Pleistocene megafauna. The contact between Strata 2 and 3 is horizontal, and is sharply demarcated by the contrast between the relatively dark brown upper portion of Stratum 2 and the relatively light colored sands of Stratum 3. Stratum 3 consists of loose white sands, muck, and peat, banded with decayed plant material. Bones from this layer are extremely abundant, stained very dark brown, and are barely permineralized. In his excavations, Weigel found no remains of extinct vertebrates in Stratum 3, except at his Locality 1, which corresponds with the area where much of the early fossil material was collected by

Weills and Ayers. According to Weigel, the beds appeared to be disturbed at Locality 1. A small creek flowed through this locality, apparently cutting through Strata 2 and 3 and mixing fossils from these beds with more recent artifacts and human bone. In six other stratigraphic sections at Vero, Weigel found no extinct vertebrates in Stratum 3 and no evidence of stream channel fills or other reworked deposits.

Owing to the presence of human remains at Vero, the age of the various strata there has raised much controversy. Weigel (1962:8-9) gave five radiocarbon dates for Stratum 2, ranging in age from 3,550 years before present (ybp) to greater than 30,000 ybp. Based on a radiocarbon date from the top of Stratum 2, Weigel (1962) hypothesized that now extinct vertebrates may have persisted in Florida until 3,500 years ago. In retrospect, it appears clear that this date is erroneous, as recent studies based on extensive series of radiocarbon dates (Meltzer and Mead 1983) suggest that no members of the extinct Pleistocene megafauna survived in North America beyond 10,000 ybp. Although no radiocarbon dates are available from Stratum 3, the absence of extinct Pleistocene megafauna and the predominance of species found in the immediate vicinity at the present time, indicate that this part of the fauna is Holocene in age. Holocene faunas are uncommon in Florida, or at least they have rarely been recognized and studied. The late Pleistocene and early Holocene Devil's Den fauna (Martin and Webb 1974), and the Nichol's Hammock fauna (Hirschfeld 1968) of unknown but probably late Holocene age, are the best known. In this paper, vertebrate fossils from Stratum 2 are regarded as late Wisconsinan (late Pleistocene, Rancholabrean), while fossils from Stratum 3, in particular the extremely rich microvertebrate sample from Weigel's Site 3a, are considered Holocene. Only four bat fossils were recovered from Stratum 2 in Weigel's excavations, the mandible he referred to *Eptesicus* sp. and three specimens of *Nycticeius humeralis*. All six species identified from Vero are present in Stratum 3, where the great majority of the bat remains occur.

METHODS AND MATERIALS

Skulls and postcranial skeletons of all 11 species of Recent bats native to Florida were available for comparison with the fossil material from Vero. Where possible, specimens from localities in southern Florida were used for comparisons. Only one maxillary fragment is present among the Vero chiropteran fossils, while mandibles are slightly more common. The most important mandibular characters used in differentiating the various species were overall size, number and form of the premolars, morphology of the molars, length of the ramus, shape of the coronoid process, and development of the masseteric fossa. Very few previous studies of bats from Florida Pleistocene localities have included

postcranial material, even though limb elements are often quite abundant in sites where bat fossils occur. In fact, two of the bat species identified from Vero are based only on postcranial material. The classic study of Miller (1907) used characters of the humerus, in addition to more conventional cranial and dental characters, to diagnose many of the higher taxonomic groups of bats. In her work on the fossil bats from the Miocene Thomas Farm Site in northern Florida, Lawrence (1943) discussed the taxonomic importance of the humerus in bats, demonstrating that almost all Recent genera of North American vespertilionids could be distinguished using characters of the proximal and distal ends of the humerus. The radius, especially the proximal end, is useful in distinguishing between certain groups of bats, although it lacks the large number of diagnostic characters found in the humerus. Terminology for various structures on the humerus and proximal end of the radius follows Vaughan (1959) and Smith (1972). Miller (1907) and Lawrence (1943) used the terms trochiter and trochin for the greater and lesser tuberosity of the humerus, respectively. However, since these structures are homologous with the greater and lesser tuberosity of other mammals, the latter terms will be used in this paper. Dental terminology is standard for mammals (Szalay 1969). Site names followed by Roman numerals refer to fossil sites listed in the Florida State Museum vertebrate paleontology locality files. Cranial and dental measurements were taken with a Gaertner measuring microscope accurate to 0.01 mm. Postcranial measurements were taken with dial calipers accurate to 0.10 mm.

All recent comparative material is from the Mammal Collection of the Florida State Museum, University of Florida (UF). The Vero fossils are from the Florida Geological Survey Collection, formerly housed in Tallahassee and now merged with the Florida State Museum Fossil Vertebrate Collection in Gainesville (UF/FGS, catalogue number preceded by V).

SYSTEMATIC PALEONTOLOGY

Order Chiroptera Blumenbach

Family Vespertilionidae Gray

Eptesicus fuscus (Palisot de Beauvois, 1796)

Referred material.—Stratum 2-V7200, partial left mandible with m_3; Stratum unknown-V7201, complete edentulous left mandible.

Recent distribution.—*Eptesicus fuscus* is one of the most widespread bats in the New World. It occurs throughout the United States, southern Canada, Greater Antilles, Bahamas, Middle America, and northern South America. In Florida, the big brown bat has been

recorded as far south as Englewood in southern Sarasota County on the west coast and from southern Highlands County in the central portion of the peninsula.

Fossil record.—Vero is the only Pleistocene fauna in Florida from which *Eptesicus fuscus* has been reported (listed as *Eptesicus* sp. by Webb 1974 and Weigel 1962). I have recently identified *E. fuscus* in two additional late Pleistocene (Rancholabrean) faunas from Florida: Arredondo IIA, Alachua County, and Monkey Jungle Hammock, Dade County. *Eptesicus fuscus* is the most widespread Pleistocene bat in North America, having been reported from more than 25 Rancholabrean faunas, ranging from Pennsylvania and Florida in the east to Wyoming and New Mexico in the west, and as far south as Nuevo Leon, Mexico (Martin 1972). This species has also been reported from a number of late Pleistocene and Holocene cave deposits in the West Indies.

Description and comparisons.—Based on their large size, the two mandibles here referred to *Eptesicus fuscus* can be distinguished from all other Florida bats except *Eumops* and *Lasiurus intermedius*. The mandible of *Eumops* differs in its larger size, reduced coronoid process, and shallow masseteric fossa. *Lasiurus intermedius* can be separated from the fossils by its shorter, more robust mandibular ramus, vertical mandibular symphysis, smaller triangular coronoid process, shallower masseteric fossa lacking a strong anterior ridge, and the more reduced m_3. The two mandibles are readily identified as *E. fuscus* by the long and relatively slender mandibular ramus, high rounded coronoid process, and deep masseteric fossa with a strong anterior ridge. Measurements of the two fossil mandibles compare closely with measurements of recent *E. fuscus* from Florida (Table 1).

Discussion.—Although single specimens of *Eptesicus fuscus* have been collected from a number of localities in the northern two-thirds of Florida, it is considered rare in the state. Likewise, *E. fuscus* is uncommon as a fossil in Florida, having been recorded from only three late Pleistocene sites based on a small handful of specimens. Most recent individuals of *E. fuscus* from Florida have been found in buildings, in association with colonies of *Tadarida brasiliensis*. According to Jennings (1958), the absence of *E. fuscus* from Florida caves is due to the high humidity and damp walls characteristic of these caves. *Eptesicus fuscus* also roosts in hollow trees and rock crevices, the former probably serving as the preferred roosting site in Florida before the appearance of man-made structures. A minimum of two individuals of *E. fuscus* is represented in the Vero deposit based on the presence of two left mandibles. The mandible from Stratum 2 represents one of the few late Pleistocene bat fossils from Vero and was the basis for Weigel's (1962:32) identification of *Eptesicus* sp. from the site.

Table 1. Comparison of mandibular measurements (in mm) of fossil bats from Vero with Recent Florida bats.[1]

	total length of mandible	alveolar length of mandibular tooth row	depth of ramus below m_2	height of coronoid process	length of m_2	width of m_2	length of m_3	width of m_3
Eptesicus fuscus								
Recent	14.5 ± 0.3	7.8 ± 0.1	2.4 ± 0.1	5.4 ± 0.2			1.7 ± 0.1	1.1 ± 0.1
	3	3	3	3			3	3
	(14.1-14.7)	(7.8-7.9)	(2.3-2.4)	(5.2-5.6)			(1.6-1.8)	(1.0-1.3)
Fossil								
V7200			2.4				1.8	1.0
V7201	14.5	7.9	2.4	5.6				
Nycticeius humeralis								
Recent	10.7 ± 0.3	5.6 ± 0.2	1.6 ± 0.1		1.3 ± 0.1	0.9 ± 0.1	1.2 ± 0.1	0.8 ± 0.1
	10	10	10		10	10	10	10
	(10.2-11.1)	(5.2-5.8)	(1.5-1.7)		(1.3-1.4)	(0.8-1.0)	(1.2-1.3)	(0.7-0.8)
Fossil								
V7228	10.6	5.6	1.7		1.3	0.9	1.2	0.8
Tadarida brasiliensis								
Recent	11.9 ± 0.4	6.6 ± 0.1	1.6 ± 0.1	3.5 ± 0.1	1.6 ± 0.1	1.2 ± 0.1	1.4 ± 0.1	1.0 ± 0.1
	10	10	10	10	10	10	10	10
	(11.2-12.6)	(6.4-6.9)	(1.5-1.7)	(3.2-3.7)	(1.5-1.7)	(1.1-1.2)	(1.4-1.5)	(0.9-1.0)
Fossil								
V7218	11.8	6.6	1.7	3.3	1.6	1.2	1.5	0.9

[1] Mean, standard deviation, sample size, and observed range (in parentheses), respectively, are given for Recent specimens.

Lasiurus intermedius H. Allen, 1862

Referred material.—Stratum 3-V7202, proximal two-thirds of left humerus; V7203, proximal end of right radius.

Recent distribution.—*Lasiurus intermedius* occurs primarily in the southeastern United States, from South Carolina to Texas, and into lowland tropical Middle America as far south as Honduras. The yellow bat is found throughout Florida, with records from as far south as Lee County on the west coast and Palm Beach, Broward, and Dade counties on the Atlantic coast (Layne 1974).

Fossil record.—*Lasiurus intermedius* is known as a fossil only from Florida. Webb (1974) recorded this species from three late Pleistocene sites in the state: Haile XIB, Alachua County; Devil's Den, Levy County; and Reddick IA, Marion County. Martin (1972) also identified *L. intermedius* from Arredondo IIA. I have recently identified a mandible of this species from the Glyptodont Site in Pinellas County.

Description and comparisons.—Based on its large size, the humerus referred to *Lasiurus intermedius* can readily be distinguished from all other Florida bats except *Eumops* and *Eptesicus*. The proximal end of the humerus differs from that of *Eptesicus* by the elliptical humeral head oriented at a 45° angle to the shaft, the more prominent greater tuberosity, and the smaller lesser turberosity. It is also readily separable from the humerus of *Eumops* by its smaller size, almost perfectly elliptical head, relatively longer and less expanded pectoral ridge, and lack of a deep groove on the lateral surface of the greater tuberosity. The fossil is identical in size and morphology to humeri of recent *L. intermedius* from Florida (see measurements in Table 2). Although the other large North American species of *Lasiurus*, *L. cinereus*, has been recorded from Florida on several occasions, it occurs there only as a rare migrant. The humerus of *L. cinereus* is larger than the fossil from Vero, with a broader proximal end and relatively thicker shaft.

As with the humerus, the proximal radius referred to *Lasiurus intermedius* needs comparison only with *Eumops* and *Eptesicus*. It is completely unlike the radius of *Eptesicus*, differing from that genus in the more robust shaft, considerably shorter ridge extending distally from the flexor fossa, lack of a deep groove in the articular surface for the capitulum of the humerus, and the acutely triangular shape of the proximalmost extension. The fossil radius can be distinguished from *Eumops* by its smaller size, more laterally placed flexor fossa, more slender shaft, relatively smaller articular surface that is rounded in outline rather than distinctly triangular, and lack of a deep central groove on the articular surface. Although essentially identical to the radius of *Lasiurus cinereus*, the fossil is somewhat smaller, as is the radius of *L. intermedius*.

Discussion.—Lasiurus intermedius roosts almost exclusively in trees and appears to be closely associated with Spanish moss (Barbour and Davis 1969). Although the yellow bat is known from more fossil sites (six) in Florida than any other bat species except *Myotis austroriparius*, it is uncommon in the sites where it occurs, generally being represented by only one or two specimens. The rarity of *L. intermedius* remains in fossil sites is not difficult to explain, because the majority of fossil chiropteran faunas in Florida are derived from deposits formed in caves, fissures, or sinkholes. Yellow bats are not known to enter caves, so apparently their presence in cave fossil deposits results from being brought into caves by predators, most likely the Barn Owl, *Tyto alba*. According to Jennings (1958), *L. intermedius* commonly feeds over water, thus providing a possible explanation for the presence of the species at Vero, based on Weigel's (1962) interpretation of the site as a pond or marsh. The two elements of *L. intermedius* identified from Stratum 3 represent one individual.

Lasiurus cf. *seminolus* (Rhoads, 1895)

Referred material.—Stratum 3-V7204, nearly complete right humerus; V7205-7206, proximal ends of right humeri; V7207, distal end of left humerus.

Recent distribution.—Lasiurus seminolus occurs primarily in the southeastern United States from North Carolina to Texas. The Seminole bat is found throughout most of Florida, as far south as Lee County on the Gulf Coast and Broward and Dade counties on the east coast.

Fossil record.—This is the first fossil record of *Lasiurus seminolus*, assuming the identification is correct. In general, the small species of *Lasiurus* have a poor fossil record. *Lasiurus borealis* has been reported from only five fossil sites: Reddick IA, Florida (although this could just as easily represent *L. seminolus*); Bat Cave, Missouri; Natural Chimneys and Clark's Cave, Virginia; and Organ-Hedricks Cave, West Virginia (Kurtén and Anderson 1980).

Description and comparisons.—The proximal humeri referred to *Lasiurus* cf. *seminolus* are readily distinguished from all Florida vespertilionids, except *Lasiurus*, by the elliptical humeral head oriented at a 45° angle to the shaft. They can be separated from the proximal humerus of *Tadarida brasiliensis*, the only similar-sized molossid in Florida, by the relatively smaller humeral head, reduced greater and lesser tuberosities, and less expanded pectoral and medial ridges. The single distal humerus agrees with *Lasiurus* and differs from all other Florida bats in the presence of a deeply excavated olecranon fossa. In addition, the fossil and *Lasiurus* can be separated from other Florida vespertilionids by the prominent distal spinous process. Unlike *Tadarida* and most other molossids in which the spinous process is free, the spinous process

Table 2. Comparison of measurements (in mm) of the humerus of fossil bats from Vero with Recent Florida bats.[1]

	total length	proximal width	thickness of shaft	width of distal articular surface
Lasiurus intermedius				
Recent		4.1 ± 0.1 13 (3.9-4.3)	1.6 ± 0.1 11 (1.4-1.8)	
Fossil				
V7202		4.1	1.7	
Lasiurus cinereus				
Recent		4.7 3 (4.6-4.8)	1.8 1	
Lasiurus seminolus				
Recent	26.8 ± 1.4 10 (24.4-28.9)	3.2 ± 0.2 16 (2.9-3.5)	1.4 ± 0.1 16 (1.2-1.6)	2.4 ± 0.1 10 (2.3-2.6)
Lasiurus cf. *seminolus*				
Fossil				
V7204	24.7		1.2	
V7205		3.1	1.4	
V7206		3.0		
V7207				2.3
Lasiurus borealis				
Recent	26.9 ± 0.9 6 (25.8-28.5)	3.3 ± 0.1 13 (3.1-3.4)	1.4 ± 0.1 10 (1.2-1.5)	2.4 ± 0.1 6 (2.3-2.4)
Nycticeius humeralis				
Recent	20.9 ± 0.9 5 (19.8-22.2)	2.9 ± 0.1 18 (2.8-3.1)	1.1 ± 0.1 17 (1.1-1.3)	2.1 ± 0.1 4 (1.9-2.2)
Fossil	20.9 2 (20.3-21.5)	3.0 ± 0.1 7 (2.8-3.2)	1.2 ± 0.1 8 (1.1-1.3)	2.3 ± 0 4 2.3

[1] Mean, standard deviation, sample size, and observed range (in parentheses), respectively, are given for Recent specimens and fossils of *Nycticeius humeralis*.

in *Lasiurus* is attached to the distal articular surface for most of its length.

The humeri referred to *L.* cf. *seminolus* are much smaller than the corresponding element in *L. intermedius* and *L. cinereus*. There are two smaller species of *Lasiurus* known from Florida, *L. seminolus* and *L. borealis*, that have humeri within the size range of the fossils. The

humeri of these two species are broadly overlapping in size (see measurements, Table 2). Examination of a series of humeri of Recent *L. borealis* and *L. seminolus* from Alachua County, Florida revealed no reliable morphological characters that would distinguish them. These species are also very similar in external and cranial morphology. They can, however, be separated by pelage color and the presence of a lachrymal ridge in *L. borealis*. Unfortunately, fossils cannot be definitely assigned to one species or the other without a skull.

Lasiurus borealis occurs primarily in the northern half of the Florida peninsula, having been recorded as far south as Hardee County, although it is not common south of Pasco County. *Lasiurus seminolus* occurs sympatrically with *L. borealis* throughout most of north Florida; however, the Seminole bat is more widely distributed in the southern half of the peninsula and is the only small *Lasiurus* presently found on the east coast of Florida as far south as Indian River County. Because the mammalian fauna from Stratum 3 at Vero closely approximates the Recent fauna of that vicinity, these fossils are tentatively referred to *L. seminolus*.

Discussion.—Like *L. intermedius*, *L. seminolus* roosts primarily in clumps of Spanish moss hanging from trees. Although *L. borealis* is not necessarily associated with Spanish moss, it too roosts almost exclusively in trees. The tree-roosting habits of these two small species undoubtedly account for their rarity in the fossil record. The occurrence of *L. borealis* or *L. seminolus* in the Reddick site is probably a result of Barn Owl predation, while the presence of *L. seminolus* at Vero is most likely related to their preference for feeding near water. Although only four fossils referable to *L. seminolus* were identified from Vero, three of these were proximal ends of right humeri representing a minimum of three individuals.

The proximal half of a right humerus (V7205), identified as *Myotis* sp. by Weigel (1962:32) and later referred to *M. austroriparius* by Webb (1974:14), is actually referable to *Lasiurus* cf. *seminolus*. The fossil differs from *Myotis* and agrees with the smaller species of *Lasiurus* in its larger size, elliptical humeral head oriented at a 45° angle to the shaft, and the reduced lesser tuberosity. The left humerus (V7204) referred to *Lasiurus* sp. by Weigel (1962:32) and later to *L. borealis* by Webb (1974:14) is a right humerus instead. I could not locate the left femur from Stratum 3 identified as *Lasiurus* sp. by Weigel.

Nycticeius humeralis (Rafinesque, 1818)

Referred material.—Stratum 2-V7228, nearly complete right mandible with m_2-m_3; V7211, nearly complete right humerus; Stratum 3-V7229, partial edentulous right mandible; V7209, complete right humer-

us; V7212, distal end of right humerus; V1603, complete left humerus; V7213-7216, V7231, proximal portions of left humeri; V7230, distal end of left humerus, V7217, one right and one left femur; Stratum unknown-V7208, nearly complete edentulous right mandible; V7210, complete right humerus; V7232, nearly complete left humerus; V7233, distal end of left humerus.

Recent distribution.—Nycticeius humeralis occurs throughout the eastern United States and along the Gulf Coast as far south as the state of Veracruz, Mexico. It is found throughout Florida and is one of the most common bats of south Florida (Jennings 1958), specimens having been taken as far south as Collier and Dade counties.

Fossil record.—The specimens of *N. humeralis* from Vero represent the first fossil record of the evening bat from Florida. The two specimens from Stratum 2 constitute the second record of *N. humeralis* from the Pleistocene of North America, the other occurrence being in Baker Bluff Cave in northeastern Tennessee (Guilday et al. 1978).

Description and comparisons,—The three mandibles referred to *N. humeralis* can be readily distinguished from *Myotis* and *Plecotus* by the presence of only two premolars, from *Pipistrellus* by their larger size, and from *Eptesicus*, *Eumops*, and *Lasiurus intermedius* by their considerably smaller size. The mandibles are generally similar in size to the two smaller species of *Lasiurus*, but they differ from them in possessing a longer, more slender mandibular ramus and a larger coronoid process, and in lacking a deep cleft between the paraconid and metaconid on all molars. The fossils can be differentiated from *Tadarida brasiliensis* by smaller size, presence of a single-rooted rather than a double-rooted P_3, strong rounded coronoid process, deep masseteric fossa, small entoconids on molars, and relatively large incisors (the incisors are small and compressed in *Tadarida*). The characters of these three mandibles, including size, length and depth of ramus, shape of coronoid process and masseteric fossa, and morphology of the dentition, agree closely with specimens of *N. humeralis* (see measurements in Table 1).

Twelve humeri from Vero are referable to *Nycticeius humeralis*. They can be separated readily from *Eptesicus* and *Eumops* by their smaller size, and from *Tadarida* and all species of *Lasiurus* by the hemispherical humeral head and reduced distal spinous process. Based on a number of characters, the humeri can easily be narrowed down to *Myotis*, *Pipistrellus*, and *Nycticeius*. The most reliable character on the proximal end of the humerus for separating the fossils from *Myotis* and *Pipistrellus* is the more prominent medial ridge extending ventrally from the lesser tuberosity and producing a larger fossa or concavity for the origin of the lateral head of the triceps muscle. In a posterior view of the proximal end, that portion of the humerus medial to the pectoral ridge

is wider in *Nycticeius* as a result of the better developed medial ridge. The distal half of the posterior surface of the humeral shaft is distinctly flattened in *Nycticeius* and the fossils, but is round in cross-section in the other two species. On the distal end of the humerus, the lateral edge of the articular surface (lateral epicondyle of the capitulum) extends lateral to the edge of the shaft in *Myotis* and *Pipistrellus*, but is in line with the shaft in the fossils and *Nycticeius*. *Nycticeius* and the fossils possess a prominent notch immediately proximal to the lateral edge of the capitulum that extends around the lateral edge almost to the anterior surface of the humeral shaft. This notch is not as well developed in the other two species. Finally, in *Nycticeius* there is a well developed, rounded tubercule on the lateral edge of the shaft just proximal to the notch, which is absent in *P. subflavus* and *M. austroriparius*. The region medial to the medial epicondyle (trochlea) is relatively large in *Myotis*, somewhat smaller in *Pipistrellus*, and very reduced in the fossils and *Nycticeius*. Therefore, although the humeri in these three species are superficially very similar, a number of characters can be used to separate them, and the fossils are clearly referable to *N. humeralis* (see measurements on humeri in Table 2).

Discussion.—Nycticeius humeralis is the most abundant fossil bat in the Vero site, with 17 identifiable elements representing a minimum of seven individuals. Evening bats roost primarily in buildings, hollow trees, and under the loose bark of trees. They seem to show a preference for cypress trees and are the common bat in Florida near cypress stands (Jennings 1958). Like the species of *Lasiurus*, *N. humeralis* is not known to enter caves, thus explaining the absence of this species from other Pleistocene sites in Florida that have produced bat fossils. Apparently, *N. humeralis* is not as subject to raptor predation as is *Lasiurus*, since species of the latter genus do on occasion appear in cave fossil deposits. Identification of fossil cypress, *Taxodium distichum*, from Stratum 3 (Berry 1917) supports Weigel's statement (1962:42) that there was a cypress pond in the vicinity of the Vero site. The presence of cypress trees and the preference of *Nycticeius humeralis* for roosting in cypress offer an explanation for the abundance of evening bat fossils at Vero.

Family Molossidae Gill

Tadarida brasiliensis (I. Geoffroy St. -Hilaire, 1824)

Referred material.—Stratum 3-V7219, proximal end of left humerus; Stratum unknown-V7218, nearly complete left mandible with m_2-m_3.

Recent distribution.—Tadarida brasiliensis is found primarily in the southern and western United States and then southward through Middle America, the West Indies, and much of South America. Brazil-

ian free-tailed bats occur throughout Florida, and according to Layne (1974) the species is the most successful bat in southern Florida, where it has been recorded as far south as Dade and Collier counties.

Fossil record.—Tadarida brasiliensis is known from three other fossil sites in eastern North America, two in Florida (Reddick IA and Nichol's Hammock) and the other in Mammoth Cave, Kentucky (outside the present range of the species). There are numerous Pleistocene records of *T. brasiliensis* from the southwestern United States and the West Indies.

Description and comparisons.—The mandible referred to *T. brasiliensis* is distinguishable from *Eumops* by its considerably smaller size and from *Pipistrellus* by its considerably larger size. The fossil differs from *Lasiurus*, *Eptesicus*, *Nycticeius*, *Myotis*, and *Plecotus* in the reduced coronoid process, shallow masseteric fossa, small compressed incisors, double-rooted p_3, and larger m_3 relative to m_2. *Myotis* and *Plecotus* both have the same number of premolar alveoli as *Tadarida*, but they possess single-rooted p_2 and p_3, while *Tadarida* lacks p_2 and has a double-rooted p_3. Based on the above combination of characters, the fossil mandible is readily identified as *T. brasiliensis* (see measurements, Table 1).

Although poorly preserved and lacking the lesser tuberosity, the proximal humerus here referred to *T. brasiliensis* is identifiable. Based on its small size and elliptical humeral head, the humerus can be distinguished from that of all Florida bats except the two small species of *Lasiurus* and *Tadarida*. The humerus is identified as *T. brasiliensis* by its broader and shorter pectoral ridge and greater distal extension of the medial ridge.

Discussion.—Only two fossils of *T. brasiliensis*, probably representing a single individual, have been identified from Vero. The Brazilian free-tailed bat is rare as a fossil in Florida, having been recorded from only three sites based on less than ten specimens. At the present time, *T. brasiliensis* in Florida roosts almost exclusively in man-made structures, such as in houses and under bridges (Jennings 1958). Although it has been observed in small numbers in several caves in Marion County, Florida (R. Franz, pers. comm.), these probably do not represent roosting colonies. In marked contrast to the southwest, where *T. brasiliensis* inhabits caves in colonies sometimes numbering into the millions, it is not known to roost in caves in the southeastern United States. Apparently, the warm humid atmosphere of Florida caves offers an unsuitable environment for roosting colonies (Jennings 1958). *Tadarida brasiliensis* in Florida has also been observed roosting under the dead fronds of palm trees in Lee and Charlotte counties in southwestern Florida, and in hollow mangrove trees in the Tampa Bay area (Jennings 1958). Palm

trees provide the natural roosting site for many species of Neotropical molossids, and it seems reasonable to hypothesize a similar roosting ecology for *T. brasiliensis* in Florida prior to the extensive construction of buildings. The probable tree-roosting habits of *T. brasiliensis*, coupled with their extremely rapid flight, would limit predation and help to explain their absence from most Florida fossil sites.

Eumops glaucinus floridanus (G. M. Allen, 1932)

Referred material.—Stratum 3-V7222, partial edentulous left mandible; V7224, proximal end of right radius; V7226, proximal end of left radius; V7227, one proximal and one distal end of femur; Stratum unknown-V7220, right maxilla with P^4-M^3; V7221, left mandible with p_3-m_3; V7223, proximal end of right humerus; V7225, proximal half of left radius.

Recent distribution.—*Eumops glaucinus* has the most restricted distribution of any bat in the United States, being known only from Charlotte and Dade counties in southernmost Florida. Wagner's mastiff bat also occurs in tropical America from southern Mexico south through Middle America, much of South America, and Cuba and Jamaica in the Greater Antilles. The species has a disjunct distribution, as it is not known to occur between southern Florida and southern Mexico.

Fossil record.—The fossil record of *E. glaucinus* is restricted to Florida, where it is known from Vero, Monkey Jungle Hammock (Martin 1977), and the late Pleistocene Melbourne fauna, Brevard County (Allen 1932; Ray et al. 1963). The fossil records from Brevard County and Indian River County (this paper) extend the known range of the species in Florida some 200 km north.

Descriptions and comparisons.—The cranial and postcranial elements here referred to *E. glaucinus* are from a very large bat, and thus need only be compared with the three largest species found in Florida—*E. glaucinus*, *Eptesicus fuscus*, and *Lasiurus intermedius*. A maxilla and partial rostrum agree with *E. glaucinus* and differ from *E. fuscus* and *L. intermedius* as follows: presence of a tiny peg-like P^3, stronger hypocone on M^1 and M^2, lack of a deeply incised nasal notch, vertical slit-like infraorbital foramen, and vertical orientation of rostrum dorsal to orbit, reflecting deep, laterally compressed snout (rostrum is dorsoventrally flattened in the two large vespertilionids). The mandible with p_3-m_3, can be differentiated from *E. fuscus* and *L. intermedius* as follows: presence of only two tiny incisors that are crowded between the canine and mandibular symphysis, double-rooted p_3, p_3 and p_4 subequal in size, and the posterior margins of trigonid and talonid on molars not at right angles to long axis of tooth row.

The proximal humerus referred to *E. glaucinus* can be readily distinguished from all other Florida bats by its very large size, teardrop-shaped humeral head oriented at a 45° angle to the shaft, short expanded pectoral ridge, and proximal extension of the greater tuberosity. The three radii are identified as *E. glaucinus* by the large, deep flexor fossa on the anterior surface just distal to the proximal articulation, the acutely triangular proximal end, and the strongly concave articular surface with a deep central groove for reception of the medial portion of the capitulum on the distal end of the humerus. The proximal and distal femur can be separated from all Florida vespertilionids by the small femoral head relative to the greater and lesser trochanters, relatively broader distal end, and more widely separated articular condyles. Among Florida bats, only *Tadarida brasiliensis* has femora with a similar morphology, but their small size eliminates them immediately.

Discussion.—Even though *Eumops glaucinus* is the second most abundant bat at Vero based on the total number of elements present (nine), a minimum of only two individuals is represented. The presence of *Eumops glaucinus* at Vero is of particular interest since this site is over 100 km north of the northernmost locality from which recent individuals of this species have been collected. A single fossil mandible of *E. glaucinus* is known from the Melbourne Site, located approximately 50 km north of Vero (Allen 1932; Ray et al. 1963). Until recently, living specimens of *E. glaucinus floridanus* had been collected only from man-made structures in the Miami area of Dade County in extreme southeastern Florida. Belwood (1981) discovered a small colony of *E. glaucinus* roosting in a hollow long-leaf pine, *Pinus palustris*, near Punta Gorda in Charlotte County on the southwest coast of Florida. Hollow trees appear to be the preferred natural roosting site of this species (Belwood 1981). The discovery of *E. glaucinus* in Charlotte County extends the modern range of the species in Florida 200 km westward and 100 km northward of Miami. With the addition of the three fossil records from Florida discussed above, the species is now known from three different localities in south Florida and two localities from the central portion of the state (Fig. 1).

Martin (1977) suggested that the presence of *Eumops glaucinus* in central Florida during the late Pleistocene represented a northward shift in winter isotherms indicative of tropical or subtropical conditions. Belwood's recent discovery of *E. glaucinus* in a part of Florida and in an ecological situation from which the species was previously unknown suggests that our knowledge of this bat is far from adequate. If *Eumops* did extend its range northward in response to warmer climates, why is it known in central Florida only from a late Wisconsinan site (Melbourne) in which climatic conditions were presumably drier and cooler than at

present, and a Holocene site (Vero) in which the climatic conditions were essentially similar to those at present? It would seem more likely that *Eumops* would have been found in one of the Sangamonian interglacial sites (Reddick, Haile, Arredondo, etc.), at a time during which climates were probably somewhat more tropical than they presently are.

As noted by Eger (1977) and Koopman (1971), the endemic Florida subspecies, *Eumops glaucinus floridanus*, is the most distinct form of the species. The Florida animal is characterized by its larger size, a feature also seen in the fossil representative of the species from Florida (see measurements in Table 3). According to Eger (1977), all Neotropical representatives of *E. glaucinus*, including those from the West Indies, are referable to the nominal subspecies, while only the Florida population is recognizable as a distinct subspecies. Baker and Genoways (1978) suggested the possibility that *E. glaucinus* invaded Florida from Cuba, a distance of only 200 km. However, the strong mainland Neotropical component of Florida's Pleistocene fauna, and the total lack of any other West Indian bats in the state, suggest strongly that the present distribution of *E. glaucinus* resulted from a warmer interglacial period when the Neotropical fauna was continuous around the Gulf Coast. Two other bats found in Florida during the late Pleistocene, *Desmodus stocki* and *Mormoops megalophylla*, also reflect this mainland Neotropical influence.

DISCUSSION

The fossil bat fauna from Vero is significant for several reasons. First, more species of bats (six) are represented at Vero than in any other fossil vertebrate fauna yet described from Florida. The two most diverse fossil chiropteran faunas from Florida listed by Webb (1974:14) were Reddick 1A, Marion County, with five species—*Desmodus stocki*, *Myotis austroriparius*, *Lasiurus borealis*, *L. intermedius*, and *Tadarida brasiliensis*—and Devil's Den, Levy County, with four species—*M. austroriparius*, *M. grisescens*, *Pipistrellus subflavus*, and *L. intermedius*. Second, among the ten or so Pleistocene and Holocene vertebrate faunas in Florida that contain abundant bat fossils, only the Vero deposit represents a depositional environment other than a cave, fissure, or sinkhole. The fossil deposits at Reddick consist of unconsolidated sediments filling caverns and solution pipes in the surrounding Eocene limestones. A cave-dwelling species, *Myotis austroriparius*, accounts for the great majority of bat remains at Reddick. The Devil's Den site is a water-filled sinkhole and cave system, presumably inhabited by the bats during a period of lower sea level and water tables in the late Wisconsinan and early Holocene. Cavernicolous bats also predominate at Devil's Den. In fact, all of the major North American Pleistocene sites listed by Kurtén and Anderson (1980) that contain large bat faunas were deposited in caves and are dominated by cave-inhabiting species.

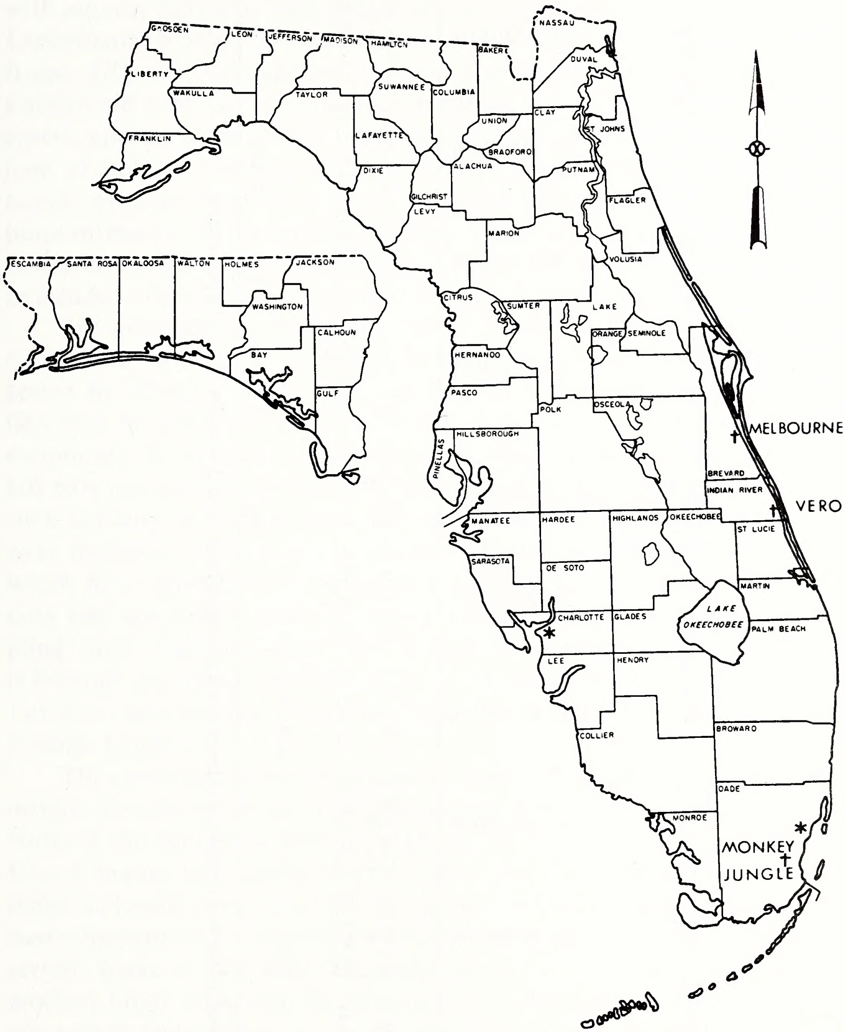

Fig. 1. Pleistocene and Recent occurrences of *Eumops glaucinus floridanus* in Florida. Asterisks (*) indicate Recent records, daggers (†) and name of fauna indicate Pleistocene records.

Based on studies of the sediments, fossil plants, and fossil vertebrates, Weigel (1962) concluded that the fossil deposits at Vero represented a pond or marsh habitat. Berry (1917) studied the fossil plants from Stratum 3 at Vero. Among the more informative plants he identified were cypress, *Taxodium distichum*, and three species of obligate pond inhabitants: water lettuce, *Pistia*; pond apple, *Anona glabra*; and water shield, *Brasenia purpurea*. A number of the other fossil plants from Vero also have aquatic tendencies. According to Weigel (1962), almost 50% of the vertebrates from Strata 2 and 3 are forms associated

Table 3. Comparison of cranial and mandibular measurements of fossil *Eumops glaucinus* from Vero with Recent *E. glaucinus* from Florida.[1]

	alveolar length of maxillary tooth row	length of M^1-M^3	length of M^1	width of M^1	length of M^2	width of M^2	depth of ramus below m_2	length of m_1	width of m_1	length of m_2	width of m_2
Eumops glaucinus											
Recent	10.0 ± 0.2 7 (9.6-10.3)	6.2 ± 0.1 7 (6.1-6.4)	2.6 ± 0.1 7 (2.5-2.6)	3.4 ± 0.1 7 (3.2-3.5)	2.5 ± 0.1 7 (2.4-2.6)	3.4 ± 0.1 7 (3.2-3.6)	2.8 ± 0.4 7 (2.3-3.2)	2.7 ± 0.1 7 (2.6-2.8)	1.8 ± 0.1 7 (1.7-1.8)	2.7 ± 0.1 7 (2.6-2.7)	1.7 ± 0.1 7 (1.7-1.8)
Fossil											
V7220	10.1	6.3	2.6	3.5	2.4	3.5					
V7221							3.1	2.7	1.8	2.7	1.7

[1] Mean, standard deviation, sample size, and observed range (in parentheses), respectively, are given for Recent specimens.

with aquatic habitats, including such obligate freshwater species as gar, *Lepisosteus*; bowfin, *Amia*; *Siren* and *Amphiuma*; two species of ranid frogs; *Alligator*; two species of water snake, *Nerodia*; four species of kinosternid mud turtles; a number of species of ducks, rails, herons, and egrets; and the round-tailed muskrat, *Neofiber alleni*. The large component of aquatic vertebrates supports the sedimentological and paleobotanical evidence that the deposits were formed in a shallow freshwater pond or marsh. Based on the presence of a number of strictly terrestrial forms in the fauna, several other habitats were certainly present in the immediate vicinity, including mesic hammock and pine flatwoods.

The presence of a diverse bat fauna at Vero is somewhat difficult to explain in the context of the freshwater pond or marsh habitat suggested by Weigel (1962). In Weigel's scenario of Vero (1962:49), "Bats flew over the pond and marsh in search of insects. . . ." It is true that bats commonly fly over open water, both in search of insects and to drink, but bats are usually absent or extremely rare in fossil deposits sampling such habitats. A large number of Pleistocene sites in peninsular Florida were deposited in marshes, swamps, or fluvial environments, several of which have abundant microvertebrate samples. Yet, except for Vero, only two specimens of fossil bats are known from Florida sites sampling such habitats—the type specimen of *Molossides floridanus* (=*Eumops glaucinus floridanus*) from Melbourne, and a mandible of *Lasiurus intermedius* from the Glyptodont Site, Catalina Gardens, Pinellas County.

The roosting ecology of the bats recorded from Vero provides some insight into the problem, as all six species are known to roost in trees. None of the bats from Vero normally roost in caves in the southeastern United States. In contrast, the two most abundant and widespread bats found as fossils in northern Florida cave and fissure deposits are *Myotis austroriparius* and *Pipistrellus subflavus*, both of which roost in caves at certain times of the year. The absence of these two species from the modern fauna of south Florida, except for accidental occurrences, is almost certainly related to the absence of dry caves south of Citrus and Marion counties.

Unlike any other Quaternary bat fauna known from Florida, Vero offers a unique view of the late Pleistocene and Holocene bat fauna associated with riparian habitats. Generally, tree-roosting bats and bats associated with freshwater habitats are rare or totally absent from fossil sites deposited in caves, fissures, or sinkholes in north Florida, as in the case of *Nycticeius humeralis* and *Eumops glaucinus*. The exact mode of deposition of the bat fossils at Vero is still a matter of speculation. Perhaps the bat carcasses accumulated in hollow trees alongside the pond or marsh and were eventually washed in when the trees fell. The great abundance of other small mammals in the Vero deposit, especially shrews and small rodents, suggests the possibility of a raptor roost in the vicinity of the pond, most likely that of *Tyto alba*.

Layne (1974) recorded seven bat species from Florida south of Lake Okeechobee. Although Vero is slightly north of this area, it is located in the southern half of the Florida peninsula. Among these seven species, *Myotis austroriparius* and *Pipistrellus subflavus* almost certainly do not breed in south Florida, and Layne considered their occurrence in the region to be accidental. The remaining five species comprise the native chiropteran fauna of south Florida: *Lasiurus seminolus*, *L. intermedius*, *Nycticeius humeralis*, *Tadarida brasiliensis*, and *Eumops glaucinus*—all of which are known from Vero. All six species of bats from Vero, including *Eptesicus fuscus*, might be expected to occur in that vicinity at the present time, with the possible exception of *Eumops glaucinus*. Apparently, the chiropteran fauna of south Florida had become established by the early Holocene and has remained essentially unchanged to the present time.

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New Trechine Beetles (Coleoptera: Carabidae) from the Appalachian Region

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ABSTRACT.— New taxa of *Pseudanophthalmus* from caves in south-central Kentucky are described and illustrated: *P. menetriesi campestris*, *P. simulans*, *pilosus*, *globiceps*, *transfluvialis*, *cerberus cerberus*, *cerberus completus*, *darlingtoni darlingtoni*, *darlingtoni persimilis*, and *pubescens intrepidus*. Two new species of *Trechus*—*T.* (*Trechus*) *caliginis* and *T.* (*Microtrechus*) *inexpectatus*—are described and illustrated from Camp Creek Bald, North Carolina/Tennessee.

The trechines are a group of small carabid beetles that includes many species restricted to cool, moist microhabitats. In the Appalachian region they are abundant in the Unaka mountain province of western North Carolina and adjacent Tennessee as well as in caves of the Appalachian Valley and Interior Low Plateaus (Barr 1979a, 1980, 1981). The following previously undescribed taxa are from both Unaka and Interior Low Plateau regions.

Pseudanophthalmus menetriesi campestris, new subspecies

Fig. 1

Etymology.— Latin *campestris*, "of the plain."

Description.— Differs from nominate *Pseudanophthalmus menetriesi* (Motschulsky) in narrower elytra, L/W for Mammoth Cave $1.56 \pm .04$ ($N = 45$) and for Walnut Hill Cave (type locality) *campestris* $1.60 \pm .04$ ($N = 45$, $P = .01$); humeri less angular, striae deeper, intervals subconvex, pubescence of pronotum and elytral discs relatively dense. Length 4.6 - 5.7, mean 5.0 ± 0.1 mm ($N = 65$). Aedeagus about as in *P. m. menetriesi*.

Type series.— Holotype male (American Museum of Natural History) and 41 paratypes, Walnut Hill Cave, 3.3 km S Park City, Barren Co., Kentucky (Park City 7½′ Quadrangle), 18 March 1966, T. C. Barr, R. M. Norton, T. G. Marsh. Measurements of holotype (mm): total length 5.20, head 0.90 long X 0.82 wide, pronotum 0.98 long X 1.05 wide, elytra 2.93 long X 1.83 wide, antenna 3.24 long.

Distribution.— This is the geographic race from the Sinkhole Plain south of Mammoth Cave National Park described but not named by Barr and Crowley (1981). It ranges from the vicinity of Hardyville, Hart

County, through Barren County to Smiths Grove and Three Forks in Warren County, Kentucky, hybridizing with nominate *menetriesi* in caves at Park City and Cave City.

Pseudanophthalmus simulans, new species

Fig. 2

Etymology.— Latin *simulans*, "simulating."

Diagnosis.— Closely similar to *menetriesi* but larger, pronotum wider, elytra pubescent over entire disc, elytral chaetotaxy +++, humeri more pronounced, with slight posthumeral sinuation in margin; aedeagus larger than that of *menetriesi*, its apex much wider in dorsal view.

Description.— Length 5.2-6.4, mean 5.8 ± 3.0 (N = 19), larger than *menetriesi* (P = .01). Form robust, convex, pubescent, elytral microsculpture not pruinose. Head as wide as long, labrum doubly emarginate. Pronotum about 0.9 as long as wide, disc pubescent, sides curved in apical 2/3, barely sinuate in basal 1/7, hind angles as in *menetriesi*. Elytra with humeri more prominent, humeral serrations larger and deeper, margin with shallow posthumeral sinuation; disc densely pubescent, posterior discal seta present. Aedeagus as in Figure 2, similar to that of *menetriesi* but significantly larger.

Type series.— Holotype male (American Museum of Natural History) and 17 paratypes, Cub Run Cave, at Cub Run, Hart Co., Kentucky (Cub Run 7½′ Quadrangle), 18 November 1964, T. C. Barr, W. M. Andrews; one paratype, same cave, 29 December 1956, L. Hubricht. Measurements of holotype (mm): total length 6.18, head 0.93 long X 0.93 wide, pronotum 1.08 long X 1.18 wide, elytra 3.50 long X 2.17 wide, antenna 3.75 long.

Distribution.— The species is an isolate known only from the type locality. Extrinsic isolation of Cub Run Cave is a reasonable hypothesis, supported by absence of any vicar taxa related to *Neaphaenops tellkampfi* (Erichson), *P. striatus* (Motschulsky), or *P. pubescens* (Horn), which coexist with *P. menetriesi*. By similar reasoning, this species and the next three (described below) are judged to have arisen along with *P. menetriesi* through multiple cave colonization by a common ancestor.

Pseudanophthalmus pilosus, new species

Fig. 3

Etymology.— Latin *pilosus*, "hairy."

Diagnosis.— Closest to *menetriesi*, differing in more convex, vaulted elytra, flat near middle of disc and with abruptly declivous sides; elytral disc uniformly pubescent and not pruinose; 6 discal striae usually deeply impressed and seriate-punctulate, intervals subconvex, discal setae +0+

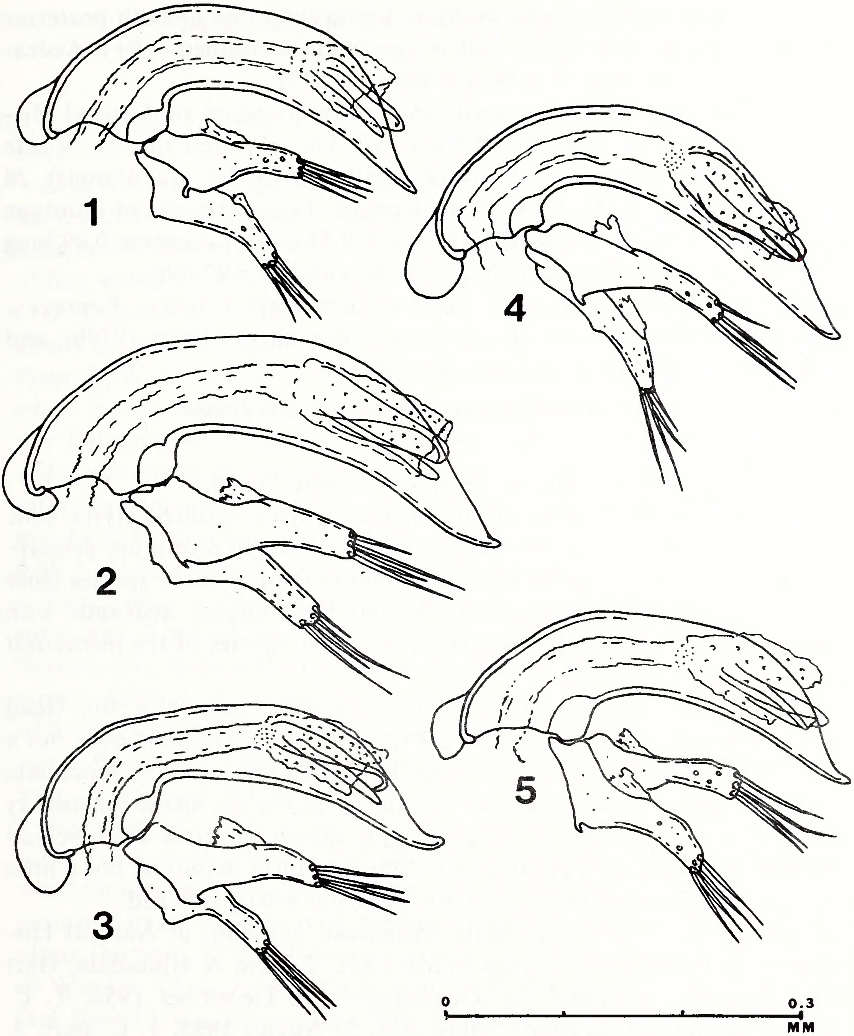

Fig. 1-5. Aedeagi of *Pseudanophthalmus* spp., left lateral view. 1: *menetriesi campestris*, n. subsp. 2: *simulans*, n. sp. 3: *pilosus*, n. sp. 4: *globiceps*, n. sp. 5: *transfluvialis*, n. sp.

in about half the individuals in most populations (except the northernmost, which are +++); pronotum wider (L/W 0.80-0.85); aedeagus straighter in middle portion, apex finely reflexed.

Description.— With the characters of *P. menetriesi* except as noted above. Length 4.4-5.7, mean 5.5 ± 0.3 mm (N = 118). Pronotum disc evidently pubescent, hind angles more consistently sharp, sometimes

with small secondary angles on base. Elytra with one or both posterior discal setae absent in about half of specimens examined (+0+). Aedeagus 0.71-0.80, mean 0.75 ± .04 mm long (N = 18).

Type series.— Holotype male (American Museum of Natural History) and 18 paratypes, Bland Cave, 1.8 km NW Spurrier on N side Akers Valley, Hardin Co., Kentucky (Millerstown 7½′ Quadrangle), 28 December 1962, T. C. Barr, R. A. Kuehne. Measurements of holotype (mm): total length 5.52, head 0.93 long X 0.74 wide, pronotum 0.99 long X 1.09 wide, elytra 3.10 long X 2.02 wide, antenna 3.97 long.

Distribution.— Limited to northwestern Hart County, Kentucky, north of the Hart County Ridge, an extrinsic barrier (Barr 1979b), and southwestern Hardin County (to Star Mills).

Pseudanophthalmus globiceps, new species
Fig. 4

Etymology.— Latin *globus*, "round," + *-ceps*, "head."

Diagnosis.— Resembles *pilosus* in very convex, vaulted elytra with dense discal pubescence, but head more rounded and pronotum proportionately wider, base more nearly rectilinear than in other species close to *menetriesi*, barely emarginate behind hind angles; aedeagus with median lobe more strongly arcuate than other species of the *menetriesi* series.

Description.— Length 4.8-5.8, mean 5.3 ± 0.3 mm (N = 10). Head and pronotum as described above. Elytra broad and quite convex but a little less so than in *pilosus*; 6-7 finely impressed and strongly punctulate striae, sutural stria deepest, intervals flat or nearly so, discal chaetotaxy normal (+++); subhumeral margin slightly sinuate, greatest width behind middle. Aedeagus of a paratype 0.73 mm, about as in *pilosus* but a little narrower and more strongly arcuate, apex not briefly reflexed.

Type series.— Holotype male (American Museum of Natural History) and 3 paratypes, Barnes Smith Cave, 5.7 km N Hinesdale, Hart Co., Kentucky (Canmer 7½′ Quadrangle), 30 December 1956, T. C. Barr; 6 additional paratypes, same cave, 30 August 1963, T. C. Barr, J. R. Holsinger; 2 July 1980, T. C. Barr, Jr., T. C. Barr, III. Measurements of holotype (mm): total length 5.84, head 1.05 long X 0.98 wide, pronotum 1.13 long X 1.23 wide, elytra 3.39 long X 2.26 wide, antenna 3.63 long.

Distribution.— Known only from the type locality, a cave at the south base of the Hart County Ridge, where *P. globiceps* coexists with *Neaphaenops tellkampfi* from the Mammoth Cave region and *P. orientalis* Krekeler, from the Greensburg area. There are few other caves in the vicinity; an interaction with *P. menetriesi* is perhaps feasible, although no suitable intervening caves have been sampled. The unusually convex elytra suggest common ancestry with *P. pilosus*, however, not *menetriesi*.

Pseudanophthalmus transfluvialis, new species

Fig. 5

Etymology.— Latin *trans-*, "across," + *fluvialis*, "pertaining to a river."

Diagnosis.— Closest to *P. menetriesi* but heavily pubescent, sides of head a little less rounded, pronotum narrower, prehumeral borders less oblique and humeri more prominent, elytral intervals subconvex instead of flat, striae distinctly impressed, disc not pruinose.

Description.— Length 4.6-5.8, mean 5.2 ± 0.3 mm (N = 32). Head about 0.15-0.18 longer than wide. Pronotum about as wide as long, mean L/W 0.96 ± .03 (N = 32); disc pubescent, hind angles as in *menetriesi*. Elytra moderately convex (not vaulted as in *pilosus* or *globiceps*, nor flattened as in nominate *menetriesi*), about 1.6 times longer than wide, pubescent; humeri stronger than in *menetriesi* (either subspecies), intervals subconvex, striae deeper, strongly punctured; chaetotaxy normal (+++) and microsculpture not pruinose. Aedeagus 0.67-0.76, mean 0.69 ± .03 mm (N = 8), closely similar to that of *menetriesi*.

Type series.— Holotype male (American Museum of Natural History) and 5 paratypes, McGinnis Cave, 4.2 km SW Bowling Green, Warren Co., Kentucky (Bowling Green South 7½′ Quadrangle), 26 September 1949, J. M. Valentine, W. B. Jones, I. C. Royer. Measurements of holotype (mm): total length 5.52, head 1.01 long X 0.86 wide, pronotum 1.09 long X 1.09 wide, elytra 3.16 long X 1.99 wide, antenna 3.43 long, aedeagus 0.76 long.

Distribution.— Described on 43 specimens from the type cave and other caves in Bowling Green (Bypass, Horseshoe, State Trooper); the westernmost limit is Wheeler Cave, 3.3 km northeast of South Union, in eastern Logan County. The species appears to have a range that runs along the base of the Dripping Spring escarpment from Bowling Green to Wheeler Cave; it does not extend south into the range of *P. princeps* (see Barr 1979b), but coexists with *Neaphaenops meridionalis* Barr and *P. loganensis* Barr in all of the caves where it has been collected (Barr 1979b). The trivial name refers to the barrier status of Barren River at Bowling Green, where the river separates *P. menetriesi*, *P. striatus*, *P. pubescens*, and *N. tellkampfi* from *P. transfluvialis*, *P. loganensis*, and *N. meridionalis*.

Pseudanophthalmus cerberus cerberus, new species and subspecies

Fig. 6

Etymology.— Named for Cerberus, the mythical dog guarding the gates of Hades, usually depicted with three or more heads; *P. cerberus* is the most widely distributed of three closely similar species in south-central Kentucky.

Diagnosis.— Similar to *P. menetriesi* in having hind angles of the pronotum tipped forward instead of produced backward (as in *striatus* and *darlingtoni*), differing in impunctate or vaguely punctulate elytral striae, strongly pruinose elytral disc, and more oblique prehumeral borders; elytral chaetotaxy +0+, the posterior discal puncture absent.

Description.— Length 4.6-5.8, mean 5.2 ± 0.3 mm (N = 77). Robust, subconvex, pubescent, elytral apical groove vestigial (diagnostic for *menetriesi* group). Head and mandibles less slender than in *menetriesi*, dorsum subglabrous; labrum with low median lobe. Pronotum 0.83-0.86 as long as wide, widest in apical third, sides rounded apical half then convergent to small, approximately right, sharp, and reflexed hind angles; anterior angles prominent, base 0.75 maximum width, apex 0.87 as wide as base; small secondary angles of base internal to very deep, oblique, basolateral impressions; median antebasal impression quite deep and linear; disc convex, with long, rather sparse pubescence; anterior marginal setae placed before greatest width, posterior marginals before hind angles. Elytra elongate-oval, 0.55-0.64 longer than wide; humeri prominent, setose with moderately coarse serrations, prehumeral borders oblique to mid-line; disc densely pubescent and strongly pruinose overall; striae rather shallow but well-defined and regular, impunctate, intervals weakly subconvex; posterior discal setae constantly absent (+0+). Aedeagus 0.97-1.13, mean 1.05 ± .05 mm long, much larger than that of *menetriesi* (or the species described above in this paper); basal bulb larger and deflexed, median lobe moderately arcuate, briefly produced, apex spout-shaped and not reflexed; transfer apparatus typical for *menetriesi* group.

Type series.— Holotype male (American Museum of Natural History) and 76 paratypes, Rhoton Cave, 3.3 km SW Hestand on N side valley of Sweetwater Creek, Monroe Co., Kentucky (Tompkinsville 7½′ Quadrangle), 7 August 1963, T. C. Barr, R. A. Kuehne. Measurements of holotype (mm): total length 5.28, head 1.02 long X 0.93 wide, pronotum 1.02 long X 1.24 wide, elytra 3.19 long X 2.05 wide, antenna 3.97.

Distribution.— Described on 279 specimens from 17 caves. The range of this taxon is roughly Y-shaped, centered in Monroe County, Kentucky, but extending northwest into southeastern Barren and southwestern Metcalfe counties, northeast to southern Adair and northwestern Cumberland counties, and south to Clay and northern Jackson counties, Tennessee, where it inhabits caves in Ordovician limestone at Central Basin level.

Pseudanophthalmus cerberus completus, new subspecies

Fig. 7

Etymology.— Latin *completus*, "complete."

Description.— Similar in size (4.6-5.4 mm) and habitus to *cerberus*

cerberus, differing in presence of both pairs of elytral discal setae (+++) and longer and straighter aedeagus (length 1.15-1.43, mean 1.30 ± 0.90 mm) with slightly reflexed tip (as in Fig. 7).

Type series.— Holotype male (American Museum of Natural History) and 11 paratypes, Cole Cave, 1.8 km N Austin, Barren Co., Kentucky (Austin 7½′ Quadrangle), 12 February 1966, T. C. Barr; 11 additional paratypes, same cave, 13 April 1973, R. Pape. Measurements of holotype (mm): total length 5.52, head 0.87 long X 0.81 wide, pronotum 0.87 long X 1.02 wide, elytra 2.76 long X 1.67 wide, antenna 3.66.

Distribution.— Described on 33 specimens, all from central Barren County, Kentucky: Cole, Beckton, Bryant Edmonds, Geralds, Mitchell, Hansons, and Slick Rock caves. Hybridization with nominate *cerberus* occurs in Bowles Branch Cave, 8.4 km southeast of Glasgow. Ranges of *P. m. campestris* and *P. c. completus* are almost parapatric, rare examples of the latter having been collected in Beckton and Hansons caves, where *P. m. campestris* is more abundant. This taxon coexists with *P. striatus* (hind angles produced; elytra not pruinose), *P. pubescens* (apical groove well developed), and *Neaphaenops tellkampfi*.

Pseudanophthalmus darlingtoni darlingtoni, new species and subspecies

Fig. 8

Etymology.— Patronymic honoring the late Philip J. Darlington, Jr.

Diagnosis.— A large species of the *menetriesi* group with shallow, impunctate striae, convex elytra with normal chaetotaxy (+++), disc weakly pruinose overall; pronotum with 1-2 long setae each side of disc and hind angles produced backward as in *P. striatus*.

Description.— Length 4.9-6.3, mean 5.7 ± 0.3 mm (N = 207). Robust, convex, pubescent. Head about 0.14 (mean index) longer than wide, dorsum subglabrous; labrum with small median lobe. Pronotum about 0.85 (mean) as long as wide, transverse-cordiform, widest in apical fourth; anterior angles scarcely produced; sides rounded apical 0.4 then convergent with very shallow or no sinuation to hind angles, which are small, sharp, and slightly obtuse; base with small, rounded, secondary angles, not obliquely inclined forward at sides (thus differing from *menetriesi* and *cerberus*); disc with scattered, rather long pubescence and 1-2 long setae each side; apex as wide as base and two-thirds greatest width. Elytra oblong-oval, very convex with deplanate circumscutellar area, 1.56 ± .04 times longer than wide (range 1.40-1.60), widest behind middle and with posthumeral marginal sinuation (as in *striatus* but deeper), humeri very prominent, prehumeral borders not quite perpendicular to mid-line, humeral serrations very coarse; disc microsculpture finely transverse, forming tight meshworks, disc with weak pruinose microsculpture over entire surface; longitudinal striae moderately and evenly impressed, rather shallow, intervals subconvex to nearly flat,

with 2-3 rows of rather long pubescence each, inner 5 striae deeper but outer striae still usually all discernible, striae impunctate, rarely evanescently punctulate; apical recurrent groove vestigial but usually faintly traceable to 5th stria, rarely to 3rd; discal chaetotaxy normal (+++). Aedeagus 0.82-1.03, mean 0.90 ± .06 mm long (N = 56); basal bulb large, forming less than right angle with main axis of median lobe, which is moderately arcuate, gradually and briefly attenuate, slightly reflexed at apex; copulatory pieces subequal in length, typical for *menetriesi* group; parameres with 4 apical setae.

Type series.— Holotype male (American Museum of Natural History) and 39 paratypes, Jones Cave, 4.3 km NNE Columbia on E side valley of Butler Branch, Adair Co., Kentucky (Cane Valley 7½′ Quadrangle), 27 July 1963, T. C. Barr. Measurements of holotype (mm): total length 5.60, head 1.07 long X 0.89 wide, pronotum 1.04 long X 1.19 wide, elytra 3.24 long X 2.02 wide, antenna 3.79 long.

Distribution.— Described on 306 specimens from 20 caves in northeastern Metcalfe, northern Adair, and southern Green counties, Kentucky. Distribution and variation in *P. darlingtoni* is discussed in detail elsewhere (Barr, in press). Hybridization with the following subspecies takes place in populations near the mouth of Little Barren River.

Pseudanophthalmus darlingtoni persimilis, new subspecies

Fig. 9

Etymology.— Latin *persimilis*, "resembling."

Description.— Length 4.8-6.4, mean 5.5 ± 0.3 mm (N = 40). Head, pronotum, and elytra more slender than in nominate *darlingtoni*; pronotum widest in apical third, usually with more pronounced antebasal sinuation, hind angles correspondingly less prominent, prehumeral borders a little more oblique to mid-line, circumscutellar depression shallower, posthumeral marginal sinuation very feeble. Aedeagus similar to that of *P. d. darlingtoni*; mean length smaller, 0.77-1.00, mean 0.87 ± .06 mm (N = 16).

Type series.— Holotype male (American Museum of Natural History) and 25 paratypes, Woodard Cave, 5.0 km NW Donansburg near Little Barren River, Green Co., Kentucky (Hudgins 7½′ Quadrangle), 22 September 1963, T. C. Barr, J. R. Holsinger, R. M. Norton. Measurements of holotype (mm): total length 5.72, head 1.04 long X 0.95 wide, pronotum 1.07 long X 1.19 wide, elytra 3.34 long X 2.11 wide, antenna 3.87 long.

Distribution.— Described on 90 specimens from 11 caves in Green County, north of Green River (a dispersal barrier upstream from the mouth of Little Barren River, where it flows in a bed of lower, cherty Fort Payne formation), and in eastern Hart County, Kentucky.

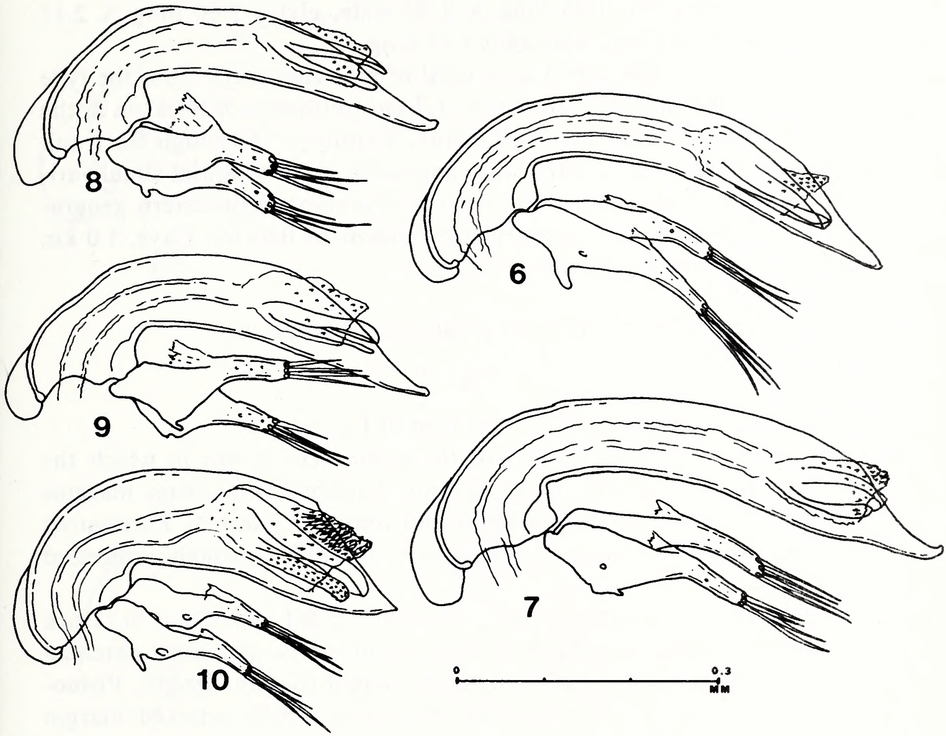

Fig. 6-10. Aedeagi of *Pseudanophthalmus* spp., left lateral view. 6: *cerberus cerberus*, n. sp. and subsp. 7: *cerberus completus*, n. subsp. 8: *darlingtoni darlingtoni*, n. sp. and subsp. 9: *darlingtoni persimilis*, n. subsp. 10: *pubescens intrepidus*, n. subsp.

Pseudanophthalmus pubescens intrepidus, new subspecies

Fig. 10

Etymology.— Latin *intrepidus*, "undaunted, intrepid."

Description.— Length 5.3-6.1, mean 5.7 mm, more robust and depressed than nominate *pubescens*. Pronotum more transverse, sides less strongly convergent and scarcely sinuate in basal half, width at base 0.75 maximum width. Elytral discal chaetotaxy consistently normal (+++), disc slightly less convex than in nominate *pubescens*, intervals quite flat. Aedeagus larger, length 1.06-1.19, mean 1.11 mm.

Type series.— Holotype male (American Museum of Natural History) and 2 paratypes, Buchanan Cave, 1.3 km W Gainesville and 30 m E KY Rt. 101, at head of hollow tributary to Difficult Creek, Allen Co., Kentucky (Scottsville 7½′ Quadrangle), 18 August 1963, T. C. Barr. Measurements of holotype (mm): total length 6.11, head 1.05 long X

1.05 wide, pronotum 1.25 long X 1.39 wide, elytra 3.60 long X 2.17 wide, antenna 4.43 long, aedeagus 1.12 long.

Distribution.— Described on a total of nine specimens from the type locality and Bryant Edmonds Cave, 1.7 km southwest of Beckton at the head of Greens Creek, Barren County, Kentucky. Although Barr and Crowley (1981) demonstrated what appears to be substantial clinal variation in *P. pubescens*, this relatively uncommon southwestern geographic race hybridizes with nominate *pubescens* in Beckton Cave, 1.0 km northwest of Beckton, Barren County.

Trechus (*Trechus*) *caliginis*, new species

Fig. 11

Etymology.— Latin *caliginis*, "of mist or fog."

Diagnosis.— A large species of the *hydropicus* group in which the aedeagal apex is simply attenuate, not knobbed; pronotum margins broadly reflexed, hind angles blunt and obtuse; closest to *T. roanicus* Barr but differing in pronotal characters and more strongly impressed elytral striae.

Description.— Length 3.9-4.2, mean 4.0 ± 0.1 mm (N = 5). Dark castaneous to reddish castaneous; legs, mouthparts, and basal antennal segments slightly paler. Eye diameter subequal to scape length. Pronotum 0.7 as long as wide, base 0.8 maximum width; reflexed margin unusually wide, sides convergent without trace of sinuosity to blunt, obtuse hind angles. Elytra very convex, 1.33 longer than wide, 5 striae present, moderately impressed but intervals either flat or very feebly convex. Aedeagus of holotype 0.52 mm long, basal bulb small and deflexed at right angle to slender, very straight median lobe, which is gradually attenuate and feebly reflexed at apex; left copulatory piece slender, rod-like, about 0.6 as long as right piece, which is hemicylindrical and bears small, irregular scallops on dorsal margin near bluntly rounded apex; parameres slender, weakly arcuate, with 3 long apical setae.

Type series.— Holotype male (American Museum of Natural History) and one male paratype, Camp Creek Bald, just below summit, elevation about 1460 m, Greene Co., Tennessee/Madison Co., North Carolina (Greystone 7½′ Quadrangle), 9 August 1983, T. C. Barr, Jr., T. C. Barr III; three female paratypes, same locality, 21 August 1960, T. C. Barr, Jr., M. C. Bowling. Measurements of holotype (mm): total length 3.96, head 0.73 long X 0.70 wide, pronotum 0.70 long X 1.01 wide, elytra 2.30 long X 1.71 wide, antenna 2.11 long, aedeagus 0.52 long.

Distribution.— At present known only from the type locality in the Bald Mountains between Greeneville, Tennessee, and Asheville, North Carolina, this species will key out near *T. roanicus* in my key to Appalachian *Trechus* (Barr 1979a); all other species of the *hydropicus* group possess a more or less knobbed aedeagal apex.

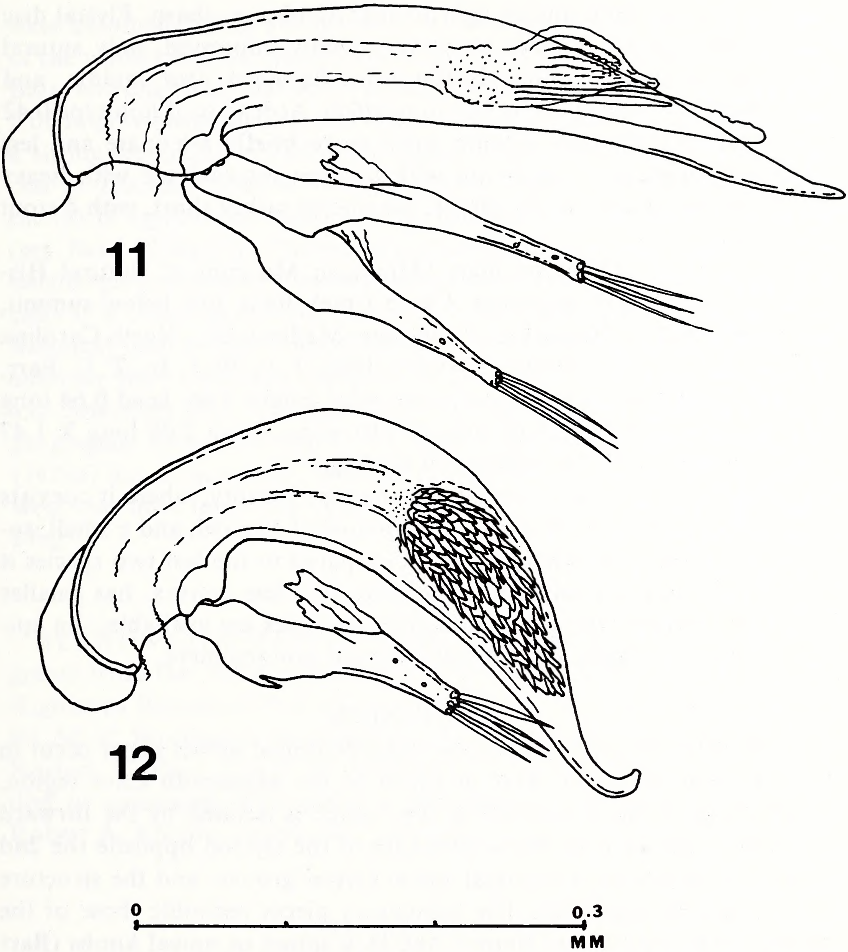

Fig. 11-12. Aedeagi of *Trechus* spp., left lateral view. 11: *T.* (*T.*) *caliginis*, n. sp. 12: *T.* (*Microtrechus*) *inexpectatus*, n. sp.

Trechus (*Microtrechus*) *inexpectatus*, new species

Fig. 12

Etymology.— Latin *inexpectatus*, "unexpected."

Diagnosis.— A species of the *uncifer* group closest to *T. uncifer* Barr, differing in larger size, more convex elytral disc with very shallow striae, and aedeagal apex less produced.

Description.— Length 3.46-3.59 mm (N = 2). Dark castaneous; legs, mouthparts, and basal antennal segments paler but not flavous as in *uncifer*, consequently less contrasting. Eye diameter less than scape length. Pronotum closely similar to that of *uncifer*: sides convergent, then almost subparallel but very briefly so, just opposite posterior mar-

ginal punctures; hind angles right to slightly obtuse, sharp. Elytral disc moderately convex, 3 inner striae very feebly impressed, only sutural complete, intervals completely flat (disc flattened near middle, and striae deep with convex intervals in *uncifer*). Aedeagus of holotype 0.42 mm long, very strongly arcuate, apex more briefly attenuate and less sharply hooked, in comparison with *uncifer*; internal sac with heavy scales obscuring copulatory pieces; parameres rather short, with 4 stout apical setae.

Type series.— Holotype male (American Museum of Natural History) and one female paratype, Camp Creek Bald, just below summit, elevation 1460 m, Greene Co., Tennessee/Madison Co., North Carolina (Greystone 7½′ Quadrangle), 9 August 1983, T. C. Barr, Jr., T. C. Barr, III. Measurements of holotype (mm): total length 3.46, head 0.64 long X 0.70 wide, pronotum 0.67 long X 1.01 wide, elytra 2.08 long X 1.47 wide, antenna 1.71 long, aedeagus 0.42 long.

Distribution.— Known only from the type locality, where it coexists with *T. caliginis*, *T. hydropicus beutenmuelleri* Jeannel, and a small isolate near *T.* (*M.*) *vandykei* Jeannel. Compared to the last two species it is distinctly larger; compared to *caliginis* it is less convex, has smaller eyes, very shallow elytral striation, and—if males are available—an apically hooked aedeagus and a single enlarged protarsomere.

DISCUSSION

All of the *Pseudanophthalmus* taxa described in this paper occur in south-central Kentucky, east or south of the Mammoth Cave region. Nine belong to the *menetriesi* group, which is defined by the forward position of the anterior discal puncture of the elytron opposite the 2nd umbilicate puncture, a vestigial apical elytral groove, and the structure of the transfer apparatus. The copulatory pieces resemble those of the *pubescens* group but are simpler and lack spines or apical knobs (Barr 1979b). The pronotum hind angles are tilted forward in *menetriesi* and its close allies (*simulans*, *pilosus*, *globiceps*, *transfluvialis*; weakest in *globiceps*) and also in *cerberus*. The hind angles are produced backward in *darlingtoni* and *striatus*. Both *cerberus* and *darlingtoni* have pruinose elytral microsculpture, which is absent in other species of the *menetriesi* group (although present to a greater or lesser extent in all species of the *pubescens* group). *Pseudanophthalmus pubescens intrepidus*, which occurs on the southern periphery of the range of polytypic *pubescens*, manages to cross the upper Barren River in the vicinity of Barren River Dam, where *Neaphaenops tellkampfi* crosses (Barr 1979b). The Barren is a barrier at Bowling Green, but not in part of its upstream course (Barr, in press).

The two larger *Trechus* species described from Camp Creek Bald

were obtained during a study of electrophoretic variation in the isolates of the *vandykei* group (*vandykei*, *pisgahensis* Barr, *tusquitee* Barr, *haoe* Barr, *bowlingi* Barr and seven undescribed species). They represent only 2 of 18 previously undescribed Appalachian *Trechus* species obtained by a sifting technique in 1982-1984 (Barr, in preparation). With four species of *Trechus*, three of them endemics, Camp Creek Bald now joins the list of eight other massifs in the Unaka region with endemic species (see Barr 1979a:41). *Trechus inexpectatus* is the only species of the *uncifer* group currently known east of the Asheville basin; morphologically it is closer to *uncifer* (Great Smokies) and *satanicus* Barr (Great Balsams) than to the series of species morphologically clustered around *aduncus* Barr (including *talequah* Barr, *howellae* Barr, *toxawayi* Barr and *coweensis* Barr; see Barr 1979a for descriptions, illustrations, and geographic ranges). Camp Creek Bald is shown on Figure 46 in Barr (1979a) but is incorrectly labeled "Camptown Bald." The site lies at the west end of a long ridge 1300-1500 m in elevation and about 10 km long.

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Fishes of Buck Creek, Cumberland River Drainage, Kentucky

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ABSTRACT.— Fifty-nine personal fish collections and museum records from thirty-nine sites in the drainage of Buck Creek, a major tributary to the upper Cumberland River below Cumberland Falls in Kentucky, revealed a total of seventy-three species and one hybrid, representing thirteen families. New records for the upper Cumberland River drainage in Kentucky included *Ictiobus bubalus*, *Ictalurus furcatus*, and *Lepomis microlophus*. *Notropis ariommus* and *Etheostoma cinereum*, two species assigned protection status in Kentucky, are known from Buck Creek, but *E. cinereum* has not been collected since 1955. Analysis of faunal resemblance of species collected at twenty-one sites along the Buck Creek mainstem revealed three faunal units. The pattern of longitudinal distribution along the mainstem involved addition of species in the middle stream section to those present in the upper section and replacement in the lower section by forms typical of low-gradient, big-river habitats.

INTRODUCTION

The upper Cumberland River basin upstream from the Tennessee border drains 13,416 sq km of eastern Kentucky (Mayes et al. 1975) and contains many of the highest quality streams remaining in Kentucky (Harker et al. 1980; Hannan et al. 1982). Although the fishes of the upper Cumberland River basin have been the subject of numerous published collections, distributional lists, and descriptions (e.g., Jordan and Swain 1883; Kirsch 1892, 1893; Woolman 1892; Evermann 1918; Jenkins et al. 1972; Starnes and Starnes 1978; Harker et al. 1979, 1980; Burr 1980; Stauffer et al. 1982), thorough ichthyofaunal surveys of tributaries within the drainage have been conducted on only the Big South Fork Cumberland River (Comiskey 1970; Comiskey and Etnier 1972) and Rockcastle River (Small 1970). Because of this paucity of information, we initiated our study of the fishes of the Buck Creek drainage. The study, based on personal collections and museum records, augments the limited published faunal information available for the drainage (Carter and Jones 1969; Harker et al. 1979, 1980).

STUDY AREA

Buck Creek, a fifth-order tributary to the Cumberland River in southeastern Kentucky (Fig. 1), drains approximately 767 sq km of Lincoln, Pulaski, and Rockcastle counties and flows south 107.2 km before discharging into the Cumberland River near river km 859. Impoundment of the river in 1951 to form Cumberland Reservoir permanently ponded several kilometers of the lower portion of Buck Creek, and this influence may extend upstream in excess of 21 km following heavy rainfall. The stream is generally less than 20 m wide and 2 m deep, but achieves a maximum width of approximately 150 m and a maximum depth exceeding 25 m near the mouth. Buck Creek is a high quality stream with clear, well-oxygenated and buffered water (Harker et al. 1979, 1980). The average stream gradient along the mainstem of the creek is 1.25 m/km and is also influenced by Cumberland Reservoir backwaters. According to the United States Army Corps of Engineers (USACE 1976), mean annual flow is 11.7 cu m/second.

Buck Creek lies almost entirely within the Eastern Highland Rim Subsection of the Interior Low Plateaus Physiographic Province (Quarterman and Powell 1978). Surface geology is composed primarily of Mississippian Age limestone deposits with limited exposures of shale bedrock in the northeastern portion of the basin. Karst topography and sinking creeks associated with limestone deposits are common in the watershed, especially south of latitude 37° 17′00″. South of Kentucky route (KY) 80 the stream is deeply entrenched within the western limit of the Cumberland Plateau Section of the Appalachian Plateaus Physiographic Province. This area, associated outlying hills to the west, and much of the extreme eastern boundary of the watershed are overlain with erosion resistant Pennsylvanian Age sandstone. Quaternary Age alluvium is limited to isolated stream channel and floodplain deposits.

Watershed land use is primarily agricultural and secondarily forest. Forested areas are small and scattered except along stream channels and in the part of the watershed south of KY 80, much of which lies within the proclamation boundary of the Daniel Boone National Forest. Coal stripmines and limestone quarries also occur in the watershed south of KY 80 and each comprises less than 1% of the watershed area. Two small (15 and 11 ha) flood control reservoirs were constructed within the Lincoln County part of the watershed by the Soil Conservation Service (T. A. Heard, pers. comm.).

MATERIALS AND METHODS

Fifty-nine collections are reported from thirty-nine collection sites in the Buck Creek drainage (Table 1, Fig. 1). Each collection site includes the stream name, locality, county, and collection date(s). Collections were made by the authors, except as noted, using seines, gill

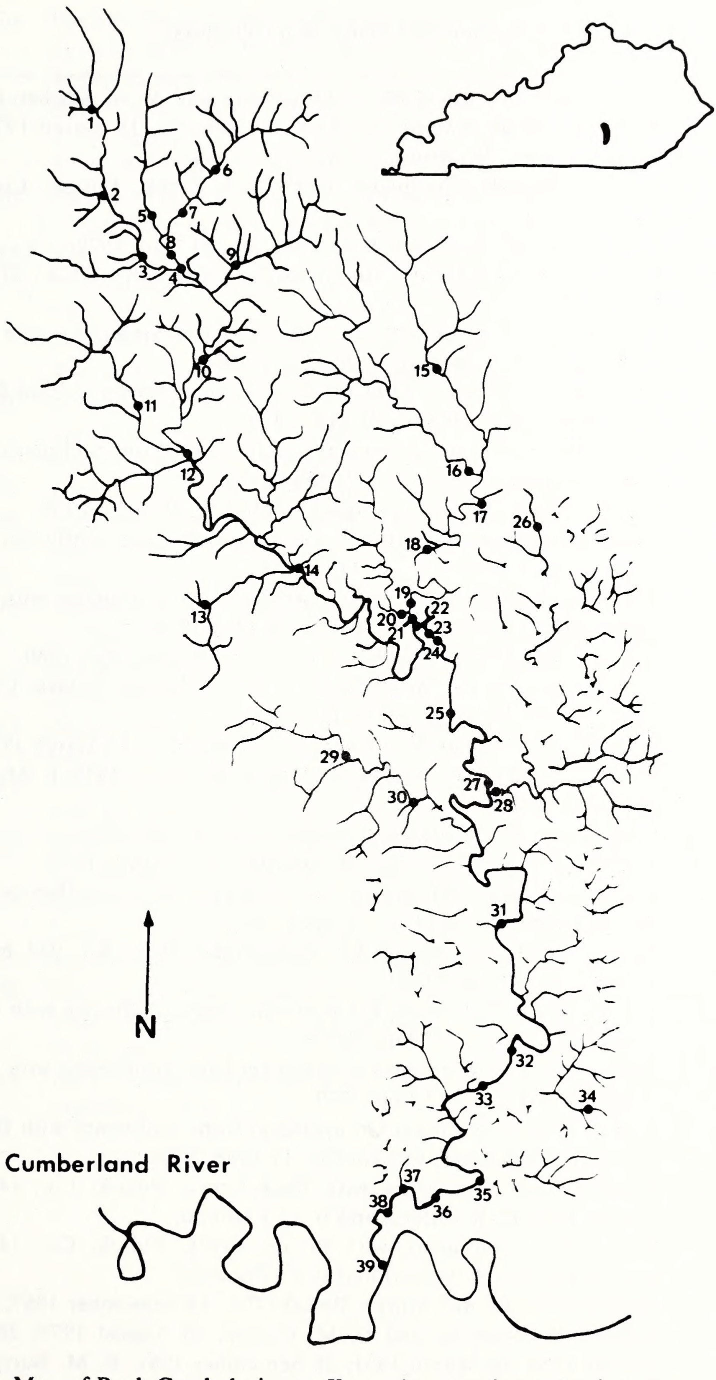

Fig. 1. Map of Buck Creek drainage, Kentucky, showing collection sites.

Table 1. Buck Creek collection sites, dates, and collectors.

Site 1.	Buck Creek, 2.7 km SSW of Ottenheim and W of Kocher Ridge Road and Maple Swamp Road jct, Lincoln Co., 14 March 1977, L. M. Page and C. W. Ronto; 29 April 1979.
2.	Buckeye Branch, confluence with Buck Creek, Pulaski Co., 29 April 1979.
3.	Buck Creek, KY 1781 bridge, Lincoln Co., 29 April 1979.
4.	Buck Creek, confluence with Gilmore Creek, Lincoln Co., 27 September 1980.
5.	Gilmore Creek, 0.5 stream km upstream from confluence with Crab Orchard Creek, Lincoln Co., 20 May 1979.
6.	Crab Orchard Creek, 1.7 km WSW of Broughtentown at Brad Petery Road bridge, Lincoln Co., 21 May 1979.
7.	Crab Orchard Creek, 1.5 stream km upstream from confluence with Gilmore Creek, Lincoln Co., 21 May 1979.
8.	Gilmore Creek, KY 1781 bridge, Lincoln Co., 29 April 1979.
9.	Glade Fork Creek, 1.5 stream km upstream from confluence with Buck Creek, Pulaski Co., 20 May 1979.
10.	Buck Creek, 0.33 stream km upstream from confluence with Bear Den Hollow tributary, Pulaski Co., 20 May 1979.
11.	Caney Creek, KY 1012 bridge, Pulaski Co., 9 November 1980.
12.	Buck Creek, 6.4 km W of Bandy at KY 70 bridge, Pulaski Co., 13 June 1970, L. M. Page and N. D. Penny.
13.	Indian Creek, 2.4 km W of Bobtown, Pulaski Co., 17 March 1976, B. M. Burr, L. M. Page, and M. A. Morris; 19 March 1978, L. M. Page and R. L. Mayden.
14.	Buck Creek, KY 39 bridge, Pulaski Co., 14 March 1981.
15.	Brushy Creek, KY 70 bridge, Rockcastle Co., 17 June 1979.
16.	Bee Lick Creek, 0.6 stream km upstream from confluence with Brushy Creek, Pulaski Co., 19 April 1981.
17.	Brushy Creek, 0.2 stream km downstream from KY 934 bridge, Pulaski Co., 19 April 1981.
18.	Brushy Creek, 5.3 stream km upstream from confluence with Clifty Creek, Pulaski Co., 17 June 1979.
19.	Brushy Creek, 0.1 stream km upstream from confluence with Clifty Creek, Pulaski Co., 17 June 1979.
20.	Clifty Creek, 0.33 stream km upstream from confluence with Brushy Creek at Elrod Road, Pulaski Co., 17 June 1979.
21.	Brushy Creek, confluence with Buck Creek, Pulaski Co., 14 September 1955, C. R. Gilbert and B. C. Franklin.
22.	Buck Creek, confluence with Brushy Creek, Pulaski Co., 14 September 1955, C. R. Gilbert and B. C. Franklin.
23.	Buck Creek, KY 461 bridge, Pulaski Co., 14 September 1967, C. R. Gilbert, W. Seaman, and C. M. Colson; 30 August 1978, 28 September 1980, 14 March 1981; 26 September 1981, B. M. Burr, S. J. Walsh, and T. E. Shepard.

24. Buck Creek, 0.61 km downstream from KY 461 bridge, Pulaski Co., 11 July 1978, S. P. Rice, E. G. Amburgey, R. C. Wilson, and J. R. MacGregor.
25. Buck Creek, KY 1677 bridge, Pulaski Co., 11 July 1978, S. P. Rice, E. G. Amburgey, R. C. Wilson, and J. R. MacGregor; 9 June 1980. A. W. Berry, M. J. Linville, J. R. MacGregor, and S. P. Rice.
26. Unnamed stream in Sinking Valley, 1.0 km E of Plato School and 1.4 km NNE of Plato, Pulaski Co., 22 November 1980.
27. Buck Creek, old KY 80 bridge at Stab, Pulaski Co., 27 July 1954, J. R. Charles; 14 September 1955, C. R. Gilbert and B. C. Franklin; 14 September 1967, C. R. Gilbert, W. Seaman, and C. M. Colson; 28 July 1973, B. A. Branson and D. L. Batch; 22 October 1976, B. M. Burr and L. M. Page; 24 June 1978, 28 October 1980.
28. Short Creek, opening to downstream cave 0.6 km ESE of old KY 80 bridge at Buck Creek, Pulaski Co., 14 September 1955, C. R. Gilbert and B. C. Franklin; 28 October 1980.
29. Flat Lick Creek, KY 461 bridge, Pulaski Co., 8 July 1979.
30. Flat Lick Creek, 1.5 km SSE of Shopville on Heron Cemetery Road and 3.2 km W of Stab, Pulaski Co., 9 November 1980.
31. Buck Creek, KY 1003 bridge, Pulaski Co., 28 September 1980.
32. Buck Creek, KY 192 bridge, Pulaski Co., 9 June 1965, R. E. Jenkins, C. Tsai, C. R. Robins, and T. Zorach; 8 September 1966, T. Zorach and R. F. Denoncourt; 19 July 1968, B. A. Branson and D. L. Batch; 28 September 1980, 9 November 1980.
33. Buck Creek, 2.5 stream km downstream from KY 192 bridge, Pulaski Co., 3 May 1981.
34. Unnamed stream in Silvers Hollow, 1.7 km NW on KY 192 from jct with KY 1003, Pulaski Co., 7 November 1981.
35. Buck Creek, 10.6 stream km downstream from KY 192 bridge and 1.6 km SSW of Poplarville, Pulaski Co., 3 May 1981.
36. Buck Creek, boat ramp off KY 1097, 8.33 stream km upstream from Cumberland River confluence, Pulaski Co., 9 November 1980.
37. Buck Creek, at Hound Hollow Creek, Pulaski Co., 26 October 1980.
38. Buck Creek, 4.6 stream km upstream from confluence with Cumberland River, Pulaski Co., 6 April 1981, 23 August 1981, 19 September 1981.
39. Buck Creek, confluence with Cumberland River, Pulaski Co., 19 September 1981.

nets, an electroshocker, and an ichthyocide. An effort was made to intensively sample all habitats at each site. Representative specimens of all except two species collected during the current survey were fixed in 10% formalin and stored in 35-40% isopropanol. Except where otherwise indicated, they are housed at the Kentucky Nature Preserves Commission pending museum deposition.

Species composition of 21 mainstem collecting sites were analyzed to determine faunal resemblance using Long's (1963) average resemblance formula, in which:

$$\text{average faunal resemblance} = C(N_1+N_2)(100)/2N_1N_2.$$

C is the number of species shared by sites 1 and 2, and N_1 and N_2 are the number of species found at sites 1 and 2, respectively. Resemblance values range from 0 to 100, where 0 indicates that sites 1 and 2 have no species in common, and 100 indicates that sites 1 and 2 have identical faunas.

RESULTS

Based on our collections, museum records, and acceptable literature records, the following fishes are known from the Buck Creek drainage. Scientific and common names and the order of presentation follow Robins et al. (1980). Distribution within the drainage is indicated by the terms "generally distributed", "occasional", and "sporadic" as defined by Smith (1965). Collection site numbers are presented for each species, followed in parentheses by the number of specimens collected (if available). Institutions where specimens are deposited and their abbreviations are as follows: Cornell University (CU), Eastern Kentucky University (EKU), Illinois Natural History Survey (INHS), University of Louisville (UL), and University of Michigan Museum of Zoology (UMMZ).

SPECIES ACCOUNTS

Petromyzontidae — lampreys

Ichthyomyzon bdellium (Jordan). Ohio lamprey. Occasional in riffles in late winter and spring. Sites: 23(1), 24(1), 27(1), 32(-).

Lepisosteidae — gars

Lepisosteus osseus (Linnaeus). Longnose gar. Carter and Jones (1969) reported one specimen from Buck Creek below the KY 80 bridge. Our specimens were collected by gill net over a sloping mud bottom from the lower mainstem where the species occurs sporadically. Site: 38(3).

Clupeidae — herrings

Dorosoma cepedianum (Lesueur). Gizzard shad. The gizzard shad was reported by Carter and Jones (1969) from two mainstem sites and was generally distributed and abundant in the lower mainstem. Sites: 32(1), 35(-), 36(3), 38(3), 39(-).

Dorosoma petenense (Günther). Threadfin shad. This species is generally distributed in downstream parts of Buck Creek influenced by Cumberland Reservoir, where it was originally introduced in 1957 as forage for game fish (Henley 1967). Sites: 38(2), 39(-).

Cyprinidae—carps and minnows

Campostoma oligolepis Hubbs and Greene. Largescale stoneroller. This species was reported from Buck Creek as *Campostoma anomalum* (Rafinesque), the central stoneroller, by Carter and Jones (1969) and Harker et al. (1979, 1980). However, Burr (1980) and Stauffer et al. (1982) indicated that the species found in the Cumberland River drainage is *C. oligolepis*. This was the most common and generally distributed species in the drainage. Sites: 1(13), 2(1), 3(5), 4(3), 5(2), 6(1), 7(4), 8(3), 9(1), 10(4), 11(2), 12(34), 13(12), 14(2), 15(1), 18(2), 19(2), 20(2), 21(5), 22(1), 23(16), 24(49), 25(3), 27(27), 28(3), 29(5), 30(1), 31(1), 32(26), 33(1), 38(1).

Cyprinus carpio Linnaeus. Common carp. Several large specimens were collected from the lower mainstem, where the species was generally distributed. Sites: 35(2), 38(1), 39(-).

Ericymba buccata Cope. Silverjaw minnow. This minnow was sporadic in the upper half of the drainage where it was also collected by Harker et al. (1979). Sites: 7(4), 11(2), 14(3), 20(3), 23(1).

Hybopsis amblops (Rafinesque). Bigeye chub. Harker et al. (1979) reported this species from the mainstem. The bigeye chub was generally distributed in the mainstem in or just downstream of riffles flowing over a variety of substrates. Sites: 22(1), 23(4), 24(-), 25(1), 27(33), 31(7), 32(5), 33(5).

Hybopsis dissimilis (Kirtland). Streamline chub. This chub was sporadically distributed in 0.3-0.6 m deep mainstem riffles with moderate current and cobble or boulder substrate. Sites: 27(1), 32(4), 33(2).

Notropis ardens (Cope). Rosefin shiner. This shiner was reported from Buck Creek by Harker et al. (1979, 1980) and was generally distributed throughout the upper half of the drainage. Sites: 1(16), 2(18), 3(13), 4(7), 5(17), 6(13), 7(7), 8(8), 9(21), 10(24), 11(9), 12(43), 14(8), 15(6), 17(8), 18(27), 21(40), 23(47), 24(14), 25(24), 27(38), 29(4), 30(4).

Notropis ariommus (Cope). Popeye shiner. This silt intolerant species (Trautman 1981) was sporadically distributed in the drainage. Site: 21(1), 32(1), 33(3).

Notropis atherinoides Rafinesque. Emerald shiner. Although this species was present in only three collections, further sampling of deep-water, riverine habitat along the mainstem would undoubtedly yield more specimens. Sites: 32(1), 33(1), 36(29).

Notropis boops Gilbert. Bigeye shiner. This shiner was sporadic in the mainstem and tributaries in the upper half of the drainage, where the species was collected from flowing pools and riffles over a generally bedrock bottom. Sites: 3(1), 8(5), 17(2), 18(6), 23(7), 24(3).

Notropis buchanani Meek. Ghost shiner. This large-river species (Smith 1979) was occasional in the lower main channel. Sites: 36(86), 37(6).

Notropis chrysocephalus (Cope). Striped shiner. Carter and Jones (1969) and Harker et al. (1979) reported the striped shiner from Buck Creek, and Harker et al. (1980) collected it in Brushy Creek. The species was generally distributed in clear pools throughout all but the lower part of Buck Creek influenced by Cumberland Reservoir. Site: 1(7), 2(5), 3(2), 4(5), 5(8), 6(2), 7(2), 8(14), 9(2), 10(10), 11(5), 12(35), 14(4), 15(6), 18(1), 21(8), 23(59), 27(4), 32(4).

Notropis galacturus (Cope). Whitetail shiner. Harker et al. (1980) reported specimens of this fish from mainstem Buck Creek. The whitetail shiner was generally distributed in the lower half of the drainage and was often collected with, but was more common than, two other species of the subgenus *Cyprinella*—*Notropis spilopterus* (Cope) and *Notropis whipplei* (Girard). *Notropis galacturus* was commonly collected from riffles flowing over gravel, cobble, or bedrock substrate and from adjacent eddy habitat. Sites: 14(7), 18(2), 19(3), 21(14), 22(5), 23(13), 24(25), 25(3), 27(44), 31(1), 32(12), 33(6).

Notropis photogenis (Cope). Silver shiner. This inhabitant of moderate to large streams (Trautman 1981) was apparently restricted to and sporadically distributed in the lower mainstem of Buck Creek upstream from the influence of Cumberland Reservoir. Sites: 27(1), 31(3), 32(19).

Notropis rubellus (Agassiz). Rosyface shiner. This shiner is generally distributed in the mainstem, where it was also collected by Harker et al. (1979). Sites: 10(2), 14(6), 23(18), 25(1), 27(19), 32(6), 33(12).

Notropis spilopterus (Cope). Spotfin shiner. The spotfin shiner was reported from the Buck Creek mainstem by Harker et al. (1979). We found it generally distributed in the lower half of the drainage exclusive of the area influenced by Cumberland Reservoir. Sites: 21(11), 23(8), 24(12), 27(1), 31(1), 32(-), 33(8).

Notropis telescopus (Cope). Telescope shiner. Harker et al. (1979, 1980) reported the telescope shiner from Buck and Brushy creeks. We found it generally distributed and readily collected from flowing pools and riffles over bedrock or gravel and cobble substrates. Sites: 2(36),

3(2), 8(13), 9(15), 10(2), 11(2), 12(3), 14(9), 15(8), 17(6), 18(10), 19(4), 20(2), 23(93), 24(-), 25(1), 27(37), 32(3).

Notropis whipplei (Girard). Steelcolor shiner. The steelcolor shiner was sporadic in the lower half of the drainage. Sites: 21(2), 32(-), 33(1).

Phoxinus erythrogaster (Rafinesque). Southern redbelly dace. This species was restricted to small headwater streams and was occasional in distribution. Sites: 4(6), 5(6), 7(1), 26(7).

Pimephales notatus (Rafinesque). Bluntnose minnow. Harker et al. (1979, 1980) reported this minnow from Buck and Brushy creeks, where it was the most abundant species. We found it to be generally distributed and one of the most common fishes in the drainage. Sites: 1(18), 2(4), 3(2), 5(1), 6(4), 7(5), 8(8), 9(4), 10(14), 11(4), 12(12), 13(4), 14(4), 15(8), 16(2), 17(3), 18(7), 19(1), 20(1), 21(13), 22(4), 23(17), 24(20), 25(6), 27(18), 29(6), 30(5), 32(-), 33(1).

Pimephales promelas Rafinesque. Fathead minnow. A first-order tributary to a sinking creek in the headwaters of Buck Creek drainage supported a small population of *P. promelas*, but probably represented a bait-bucket introduction. Site: 26(2).

Pimephales vigilax (Baird and Girard). Bullhead minnow. This inhabitant of medium and large streams (Smith 1979) was sporadically distributed in the lower mainstem. Site: 37(2).

Rhinichthys atratulus (Hermann). Blacknose dace. This species was occasional in small headwater streams over gravel substrates. Sites: 1(6), 4(1), 6(1), 9(1), 13(3), 29(9).

Semotilus atromaculatus (Mitchill). Creek chub. This chub was generally distributed and common throughout the upper half of the drainage and present in tributaries in the remainder. Harker et al. (1980) reported specimens from Brushy Creek. Sites: 1(5), 2(2), 4(1), 5(5), 6(4), 7(2), 8(2), 9(3), 10(3), 18(2), 20(3), 21(2), 23(1), 24(2), 26(2), 28(1), 29(1), 30(1), 34(3).

Catostomidae—suckers

Carpiodes cyprinus (Lesueur). Quillback. The quillback occurs sporadically in the lower mainstem of Buck Creek influenced by Cumberland Reservoir. The specimen retained (EKU 1190) measured 35 cm standard length (SL), and was taken by gill net over a mud and debris bottom in water less than 9.1 m deep. Sites: 35(1), 38(2).

Carpiodes velifer (Rafinesque). Highfin carpsucker. Two adult specimens, one (EKU 1190) of which measured 34 cm SL, were taken by gill net from the lower mainstem, where the species occurs sporadically. Site: 38(2).

Catostomus commersoni (Lacepède). White sucker. The white sucker was sporadic in tributaries of Buck Creek. Sites: 2(1), 6(1), 30(1).

Hypentelium nigricans (Lesueur). Northern hog sucker. Carter and Jones (1969) reported this species from all three sites they sampled on Buck Creek, and Harker et al. (1979, 1980) reported specimens from the mainstem and Brushy Creek. The northern hog sucker was generally distributed throughout all but the lower mainstem of Buck Creek and was the most common catostomid in the drainage. Sites: 1(2), 5(2), 6(1), 7(1), 11(1), 12(9), 14(3), 15(1), 18(1), 21(1), 23(5), 24(11), 27(2), 29(2), 30(1), 32(5), 33(1).

Ictiobus bubalus (Rafinesque). Smallmouth buffalo. Three specimens of this typically large-river buffalo (Smith 1979) were collected by gill net from the lower mainstem, where the species occurred sporadically. One specimen was retained (EKU 1190) and measured 39 cm SL. Site: 38(3).

Moxostoma anisurum (Rafinesque). Silver redhorse. One specimen measuring 17.6 cm SL was collected from Buck Creek in 1954 by J. R. Charles (UL 6865) (R. E. Jenkins, pers. comm.); however, exact locality information was not recorded. Site: unknown.

Moxostoma carinatum (Cope). River redhorse. Although the river redhorse has been reported to inhabit medium-size rivers with gravel and rock bottoms and swift or strong flow (Pflieger 1975; Smith 1979), our specimens were collected from the sluggish lower mainstem, where the species occurs sporadically. The specimen collected at Site 35 was taken by gill net in 3.0 m of slowly flowing water over a bottom that graded from mud and debris to rock. Sites: 35(1), 38(3).

Moxostoma duquesnei (Lesueur). Black redhorse. Harker et al. (1979, 1980) reported specimens of this sucker from the mainstem and Brushy Creek. The black redhorse was occasional throughout the Buck Creek drainage. Sites: 3(1), 11(1), 16(1), 24(-), 27(1), 35(2).

Moxostoma erythrurum (Rafinesque). Golden redhorse. Carter and Jones (1969) collected 112 specimens from three sites on the mainstem, some of which were probably misidentified in light of the diverse sucker fauna present in Buck Creek. This was the most generally distributed and common *Moxostoma* in the drainage. Sites: 7(2), 18(2), 19(2), 21(3), 22(8), 23(8), 24(-), 27(4), 33(1).

Moxostoma macrolepidotum (Lesueur). Shorthead redhorse. Only one specimen of the subspecies *M. macrolepidotum breviceps* (CU 52283) has been collected from the drainage (R. E. Jenkins, pers. comm.). Site: 32(1).

Ictaluridae—bullhead catfishes

Ictalurus furcatus (Lesueur). Blue catfish. Several specimens of the blue catfish were collected from the lower mainstem, where the species occurs occasionally. Site: 38(-).

Ictalurus natalis (Lesueur). Yellow bullhead. Carter and Jones (1969) reported a specimen from the mainstem near the KY 39 bridge. Three juvenile specimens of this sporadically distributed species were collected from a drought isolated pool. Site: 4(3).

Ictalurus punctatus (Rafinesque). Channel catfish. One specimen was reported from the mainstem at the KY 80 bridge by Carter and Jones (1969). Although the channel catfish was collected only from the lower mainstem, it is probably widely distributed in the drainage. Sites: 35(1), 38(5).

Noturus flavus Rafinesque. Stonecat. Carter and Jones (1969) reported a specimen of *N. flavus* from the mainstem at the KY 70 bridge. The stonecat was occasional in the lower mainstem exclusive of the area influenced by Cumberland Reservoir. Recent monthly collections at Sites 14, 19, and 32 yielded a dozen additional specimens from under slab boulders and cobble in areas of moderate to swift current. Sites: 21(3), 23(3), 24(-), 25(-), 32(-).

Pylodictis olivaris (Rafinesque). Flathead catfish. Only one specimen was collected from the mainstem; however, the flathead catfish is probably more common and widely distributed along the mainstem. Site: 38(1).

Cyprinodontidae—killifishes

Fundulus catenatus (Storer). Northern studfish. Harker et al. (1979, 1980) reported the northern studfish from Buck and Brushy creeks. We found it common and generally distributed in the upper part of the drainage. Sites: 1(14), 2(4), 3(1), 4(4), 5(2), 6(2), 7(4), 8(5), 9(3), 10(1), 11(2), 12(24), 14(1), 15(2), 16(1), 17(1), 19(2), 20(1), 21(2), 23(12), 24(4), 27(2), 32(1).

Atherinidae—silversides

Labidesthes sicculus (Cope). Brook silverside. The brook silverside was generally distributed in the lower mainstem. Sites: 23(1), 31(2), 32(1), 36(2), 38(2).

Percichthyidae—temperate basses

Morone chrysops (Rafinesque). White bass. Although only one specimen was collected during the survey, Carter and Jones (1969) stated that white bass are harvested by fishermen from Buck Creek near Cumberland Reservoir. Site: 38(1).

Morone saxatilis (Walbaum). Striped bass. This introduced game fish has been stocked in Cumberland Reservoir essentially every year since 1957 (Axon et al. 1982) and, according to a local boat dock operator, is sporadically harvested by anglers from the lower, impounded section. Site: none.

Centrarchidae—sunfishes

Ambloplites rupestris (Rafinesque). Rock bass. The rock bass was reported from the mainstem by Carter and Jones (1969) and Harker et al. (1979) and from Brushy Creek by Harker et al. (1980). It was generally distributed in all but the lower impounded mainstem. Sites: 11(1), 14(1), 15(1), 21(2), 23(4), 24(6), 25(1), 27(3), 29(1), 32(2).

Lepomis cyanellus Rafinesque. Green sunfish. This sunfish was reported by Carter and Jones (1969) and Harker et al. (1979, 1980), and was generally distributed and common in pools throughout the drainage. Sites: 1(1), 5(1), 6(1), 7(2), 8(1), 9(1), 11(1), 15(2), 16(1), 21(1), 24(2), 27(1), 34(3).

Lepomis gulosus (Cuvier). Warmouth. This species was generally distributed in the lower half of the drainage. Sites: 18(1), 32(-), 36(1), 37(2), 38(-).

Lepomis humilis (Girard). Orangespotted sunfish. In Kentucky, this sunfish is sporadic in all but the extreme western part of the state (Burr 1980). Seven specimens (INHS 76015) were collected from a Buck Creek headwater site (L. M. Page, pers. comm.). Site: 1(7).

Lepomis macrochirus Rafinesque. Bluegill. The bluegill was reported from Buck Creek by Carter and Jones (1969) and Harker et al. (1979, 1980). This game fish was generally distributed and common throughout the drainage. Sites: 1(13), 2(3), 4(1), 6(4), 7(1), 8(2), 9(1), 10(2), 12(3), 15(1), 18(1), 21(2), 23(5), 24(1), 25(1), 27(2), 29(2), 31(1), 33(1), 35(1), 36(11), 37(1), 38(3), 39(-).

Lepomis megalotis (Rafinesque). Longear sunfish. Generally distributed and common throughout the drainage, the longear sunfish was previously reported by Carter and Jones (1969) and Harker et al. (1979, 1980). Sites: 1(3), 2(3), 3(4), 7(1), 10(2), 11(1), 12(4), 14(1), 17(1), 19(1), 21(4), 22(3), 23(4), 24(4), 25(2), 27(7), 32(-), 37(2), 38(10).

Lepomis macrochirus x *Lepomis megalotis*. This is a relatively common natural hybrid (Trautman 1981). Site: 23(1).

Lepomis microlophus (Günther). Redear sunfish. One adult specimen of *L. microlophus* was collected from the lower mainstem. As suggested by Burr (1980) in regard to other eastern Kentucky records, this may have resulted from an introduction. Site: 38(1).

Micropterus dolomieui Lacepède. Smallmouth bass. Previously reported from two mainstem Buck Creek sites by Carter and Jones (1969), the smallmouth bass was generally distributed and common throughout the drainage. Sites: 1(1), 2(1), 9(1), 18(1), 23(3), 24(5), 27(2), 32(3), 38(1).

Micropterus punctulatus (Rafinesque). Spotted bass. Carter and Jones (1969) reported the spotted bass from all three mainstem sites

they surveyed. This species was common and generally distributed in the drainage. Sites: 15(1), 19(1), 21(1), 22(1), 23(4), 24(5), 27(3), 31(2), 32(2), 36(7), 37(3), 38(1).

Micropterus salmoides (Lacepède). Largemouth bass. Although reported by Carter and Jones (1969) from a mainstem site and by Harker et al. (1980) from Brushy Creek, the largemouth bass was sporadic in Buck Creek and was collected only from the lower mainstem during our survey. Sites: 32(-), 38(1).

Pomoxis annularis Rafinesque. White crappie. This species was generally distributed and abundant in the lower mainstem influenced by Cumberland Reservoir. Sites: 32(-), 35(2), 38(2), 39(-).

Percidae—perches

Etheostoma blennioides Rafinesque. Greenside darter. Harker et al. (1979, 1980) reported this species from Buck and Brushy creeks. This darter was generally distributed but seldom abundant within the drainage, and was absent from the part influenced by Cumberland Reservoir. Adults were usually collected from substrates that ranged from coarse gravel to boulder riffles with moderate current. Sites: 2(1), 3(2), 5(1), 6(1), 7(3), 8(1), 10(1), 13(1), 15(1), 17(1), 18(1), 19(1), 21(1), 23(3), 24(1), 25(2), 27(45), 31(1), 32(15), 33(1).

Etheostoma caeruleum Storer. Rainbow darter. The rainbow darter was reported by Harker et al. (1979, 1980) from Buck and Brushy creeks. It was the most common and widely distributed darter in the drainage. Collections were made over substrates ranging in size from medium gravel to cobble in slow to moderate current. Sites: 1(26), 2(6), 3(3), 4(2), 5(9), 6(5), 7(3), 8(3), 9(1), 10(5), 11(2), 12(14), 13(2), 14(2), 15(1), 17(4), 18(5), 19(1), 20(2), 21(1), 22(2), 23(36), 24(26), 25(5), 27(14), 31(1), 32(17), 33(2).

Etheostoma camurum (Cope). Bluebreast darter. Harker et al. (1979) reported the bluebreast darter from Buck Creek. It was generally distributed in the swiftest areas of mainstem riffles where substrates varied from coarse gravel to boulders, and was often collected with *Etheostoma maculatum* Kirtland, another species of the subgenus *Nothonotus.* Sites: 12(1), 19(7), 23(3), 24(4), 25(8), 27(1), 31(2), 32(24), 33(3).

Etheostoma cinereum Storer. Ashy darter. This darter is known from Buck Creek as a result of one specimen collected in 1954 (UL 5392) and seven specimens collected in 1955 (UMMZ 171557, 171590) (B. M. Burr, pers. comm.; C. R. Gilbert, pers. comm.). Sites: 22(2), 27(6).

Etheostoma flabellare Rafinesque. Fantail darter. This darter was reported by Harker et al. (1979, 1980) from Buck and Brushy creeks. It was generally distributed in moderate to swift riffles and flowing pools

over fine to coarse gravel in the upper half of the drainage. Sites: 1(6), 2(4), 3(2), 5(3), 6(2), 7(1), 8(2), 9(1), 10(2), 12(24), 13(1), 14(1), 15(2), 17(1), 18(1), 19(2), 21(3), 23(38), 24(9).

Etheostoma maculatum Kirtland. Spotted darter. This species was generally distributed in the lower half of the drainage and often occurred with *E. camurum* under large slab boulders in moderate to swift current. Harker et al (1979) previously reported the spotted darter from Buck Creek. Sites: 14(3), 19(2), 23(6), 24(1), 25(12), 27(14), 31(1), 32(25), 33(1).

Etheostoma spectabile (Agassiz). Orangethroat darter. One somewhat aberrant specimen (INHS 87624) (L. M. Page, pers. comm.) was collected from a small, headwater tributary. Site: 2(1).

Etheostoma stigmaeum (Jordan). Speckled darter. Harker et al. (1979, 1980) reported the speckled darter from Buck and Brushy creeks. It was generally distributed and was often collected in sluggish runs over a silty-sand substrate. However, adults were occasionally taken from the margins of coarse gravel riffles. Sites: 1(4), 3(5), 5(1), 8(1), 10(7), 12(5), 14(3), 16(1), 21(3), 22(2), 23(5), 24(8), 25(5), 27(6), 31(2), 32(5).

Etheostoma virgatum (Jordan). Striped darter. Harker et al. (1979, 1980) reported this species from Buck and Brushy creeks. The striped darter was generally distributed and, as reported by Page and Schemske (1978), is the only slab-pool *Catonotus* occupying the drainage. Sites: 1(20), 3(7), 4(2), 5(3), 7(1), 8(1), 10(2), 11(1), 12(1), 14(3), 15(1), 16(2), 17(2), 18(1), 20(1), 21(7), 22(1), 23(5), 24(7), 25(1), 27(4), 29(2).

Etheostoma zonale (Cope). Banded darter. The banded darter was occasional in the mainstem of lower Buck Creek. We collected it from the interstices of gravel over swift, boulder and bedrock riffles. Sites: 23(1), 24(3), 25(2), 27(6), 32(11).

Percina caprodes (Rafineque). Logperch. The logperch was reported from mainstem Buck Creek by Carter and Jones (1969) and Harker et al. (1979). Generally distributed along the Buck Creek mainstem, it was collected from a variety of habitats ranging from swift, cobble and boulder riffles to a slow flowing, silt covered bedrock pool. Sites: 10(2), 19(1), 22(1), 23(1), 24(2), 25(2), 27(4), 31(1), 32(13), 33(2), 36(2), 37(1).

Percina maculata (Girard). Blackside darter. Since the only collections of this percid were two made in 1955 (C. R. Gilbert, pers. comm.), the species is either sporadically distributed or possibly extirpated from Buck Creek. Sites: 21(1), 27(1).

Stizostedion canadense (Smith). Sauger. This species was apparently sporadic in the lower mainstem of Buck Creek where, according to a local boat dock operator, it is harvested irregularly by fishermen. Site: none.

Stizostedion vitreum (Mitchill). Walleye. According to a local boat

dock operator, fishermen sporadically harvest walleye from the lower mainstem. Site: 38(1).

Sciaenidae—drums

Aplodinotus grunniens Rafinesque. Freshwater drum. This primarily large-river fish (Smith 1979) was reported by Carter and Jones (1969) and was generally distributed in the lower mainstem. Sites: 32(1), 38(2), 39(-).

Cottidae—sculpins

Cottus carolinae (Gill). Banded sculpin. The banded sculpin was reported by Harker et al. (1979) and was occasional in moderate to swift riffles containing cobble and boulders. Sites: 25(1), 27(5), 28(7), 32(10), 33(1).

DISCUSSION

Seventy-three species of fishes and one hybrid, representing 13 families, were found to occur in the Buck Creek drainage. Approximately 80% consisted of members of the Cyprinidae (23 species), Percidae (14), Centrarchidae (11), and Catostomidae (10). Of the 121 species reported by Burr (1980) from the upper Cumberland River drainage in Kentucky, 70 are known to occur in Buck Creek. Of the remaining 51 species, 21 are known from adjacent streams or Cumberland Reservoir and potentially occur in Buck Creek (Table 2).

New distributional records were obtained for *Ictiobus bubalus*, *Ictalurus furcatus*, and *Lepomis microlophus* in the upper Cumberland River drainage, and the continued existence of *Carpiodes velifer* within the drainage was confirmed. Within the Cumberland River drainage, *Ictiobus bubalus* was formerly known to occur only in the lower part of the river in western Kentucky, which has been impounded to create Barkley Reservoir (Burr 1980; Lee 1980). Our collection extends the known range of *I. bubalus* in the Cumberland River upstream approximately 854 km from the nearest downstream collection made at river km 4.8 (D. A. Etnier, pers. comm.). *Ictalurus furcatus* had not previously been collected from the upper Cumberland River drainage of Kentucky (Burr 1980). It was not entirely unexpected, however, since specimens have been taken from the river in adjacent Tennessee (Glodek 1980; D. A. Etnier, pers. comm.). *Lepomis microlophus* is sporadic and uncommon throughout the state, except in the upper Cumberland River drainage (Burr 1980). Although the specimen from Buck Creek represents the first record for the upper Cumberland River drainage, the redear sunfish has been widely stocked in impoundments and is probably not native to the drainage. *Carpiodes velifer* is sporadically distributed in the eastern half of Kentucky (Burr 1980) and was previously

known from the upper Cumberland River drainage as a result of two 1925 collections deposited at UMMZ (B. M. Burr, pers. comm.). The highfin carpsucker persists in the upper Cumberland River drainage despite extensive habitat alteration resulting from impoundment of 162 km of the mainstem Cumberland River and pollution from coal mining. These records lend credence to speculation that other fishes, especially large-river forms, may be collected from the Buck Creek drainage (Table 2), and emphasize the need to sample such habitat during faunal surveys.

A total of 14 specimens of *Ericymba buccata* was collected from five sites in the Buck Creek drainage by Harker et al. (1979) and during this survey. Moreover, four additional specimens (EKU 1215) were recently collected from the adjacent Pitman Creek drainage, Pulaski County. These new records significantly expand the range of the silverjaw minnow in the upper Cumberland River drainage as depicted by Burr et al. (1980) and Gilbert (1980a). Buck Creek has been rather well collected (B. M. Burr, pers. comm.), which suggests that the silverjaw minnow has only recently dispersed into the Buck and Pitman creek drainages. However, its current distribution closely approximates the upper Cumberland River drainage on the Cumberland Plateau before the upstream migration of Cumberland Falls, suggesting that the species was simply overlooked by previous investigators. According to McGrain (1966), Cumberland Falls originated on the Pottsville escarpment near Burnside, Kentucky, and has eroded into the Cumberland Plateau approximately 72 km to its present location. Prior to the retreat of the falls, Buck Creek was the most downstream major tributary to the Cumberland River above the falls, while Pitman Creek and Big South Fork Cumberland River discharged below the falls. Thus, *E. buccata* is now known to occupy all major tributaries to the Cumberland River upstream from the apparent original location of Cumberland Falls. Although it may have been introduced into Buck and Pitman creeks via bait bucket transfer, Burr et al. (1980) mentioned evidence of recent range expansion by the silverjaw minnow in other states and discussed the implications of several newly discovered, isolated populations in the lower Green and Tradewater rivers of Kentucky.

Several alternative mechanisms for the dispersal of *E. buccata* into Buck and Pitman creeks are available. The first involves movement through subsurface channels, which potentially connect Buck Creek with adjacent drainages. Karst topography including numerous sinkholes and subterranean streams is common in the Buck Creek drainage and extends east and northeast to the Dix and Rockcastle river drainages and west to the Pitman Creek drainage. *Ericymba buccata* is present in the Dix River and western tributaries to the Rockcastle River (Burr et

Table 2. Species that potentially occur in Buck Creek, their locality of occurrence and source.

Species	Locality of occurrence	Source
Ichthyomyzon greeleyi	Little South Fork	Comiskey and Etnier (1972)
Lampetra aepyptera	Taylor Branch, Youngs Creek, and Clear Creek	Walsh and Burr (1981)
Acipenser fulvescens	Cumberland River	Burr (1980)
Polyodon spathula	Cumberland Reservoir	Henley (1967), Charles et al. (1979), Axon et al. (1980)
Anguilla rostrata	Statewide	Burr (1980)
Hiodon alosoides	Cumberland River	Gilbert (1980b)
Hiodon tergisus	Cumberland Reservoir	Henley (1967), Charles et al. (1979), Axon et al. (1980, 1982)
Esox americanus	Cumberland Reservoir	Henley (1967)
Carassius auratus	Cumberland Reservoir	Henley (1967)
Hybopsis storeriana	Cumberland River	Gilbert (1980c)
Notropis leuciodus	Fishing Creek Little South Fork	Harker et al. (1980) Comiskey and Etnier (1972)
Notropis volucellus	Rockcastle River Rock Creek Little South Fork	Gilbert and Burgess (1980) Harker et al. (1979) Harker et al. (1979)
Notropis sp. (undescribed sawfin shiner)	Pitman Creek Big South Fork	Warren (1981) Burr (1980)
Carpiodes carpio	Cumberland River	Burr (1980)
Ictiobus cyprinellus	Obey River Wolf Creek	Lee and Shute (1980) Burr (pers. comm.)
Minytrema melanops	Cumberland Reservoir	Henley (1967)
Ictalurus melas	Cumberland Reservoir	Henley (1967)
Fundulus notatus	Cumberland Reservoir	Henley (1967)
Gambusia affinis	Cumberland Reservoir Upper Cumberland River	Henley (1967) Burr (1980)
Pomoxis nigromaculatus	Cumberland Reservoir	Henley (1967), Charles et al. (1979), Axon et al. (1980, 1982)
Percina sciera	Pitman Creek Big South Fork	Page (1980) Page (1980)

Table 3. Average resemblance values (%) calculated for faunas at 21 Buck Creek mainstem collecting sites.

	1	2	3	4	10	12	14	21	22	23	24	25	27	31	32	33	35	36	37	38	39
1	X	63	65	60	73	78	59	65	31	65	64	44	58	26	39	28	9	9	20	20	11
2	X	X	69	55	78	69	56	60	30	64	60	47	53	28	42	30	10	10	21	22	12
3	X	X	X	49	80	79	72	62	46	67	68	55	61	29	45	25	10	0	11	11	0
4	X	X	X	X	61	57	45	53	26	49	43	35	42	24	24	22	11	11	12	13	13
10	X	X	X	X	X	80	73	68	51	75	67	67	65	40	50	40	9	19	31	16	11
12	X	X	X	X	X	X	78	68	46	72	68	61	66	36	50	31	10	10	21	17	12
14	X	X	X	X	X	X	X	65	43	77	65	65	67	33	56	39	0	0	10	10	10
21	X	X	X	X	X	X	X	X	56	73	75	55	65	45	52	52	8	17	28	17	10
22	X	X	X	X	X	X	X	X	X	63	64	60	68	54	50	48	0	21	34	19	0
23	X	X	X	X	X	X	X	X	X	X	90	77	80	67	71	59	8	31	35	22	10
24	X	X	X	X	X	X	X	X	X	X	X	75	83	63	64	56	16	24	35	19	10
25	X	X	X	X	X	X	X	X	X	X	X	X	76	61	66	62	9	18	29	14	11
27	X	X	X	X	X	X	X	X	X	X	X	X	X	66	73	66	16	23	35	18	10
31	X	X	X	X	X	X	X	X	X	X	X	X	X	X	64	62	10	39	32	23	12
32	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	68	15	38	34	31	19
33	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	9	27	20	9	11
35	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	38	13	58	58
36	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	67	42	29
37	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	37	15
38	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	62
39	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

al. 1980; Gilbert 1980a; Branson and Batch 1981) and could have actively or passively moved via subsurface channels into Buck Creek and from there into Pitman Creek. Dispersal through Cumberland River Reservoir constitutes the second mechanism. Guillory (1978) discussed active and passive dispersal via the main channel of the lower Mississippi River by *Notropis longirostris* (Hay), a small-stream species. Burr et al. (1980) interpreted the presence of *E. buccata* in the Green River main channel as evidence of direct dispersal to tributary streams. The final mechanism, stream capture, is plausible, but potential sites of piracy with adjacent drainages could not be identified. Whether *E. buccata* is expanding its range or is limited to the Cumberland River drainage on the Cumberland Plateau and Pitman Creek can only be determined by periodic surveys of the Fishing Creek and Big South Fork Cumberland River fish faunas, which apparently do not currently include this species (Comiskey and Etnier 1972; Harker et al. 1980).

Two species assigned protection status in Kentucky by the Kentucky Academy of Science (Branson et al. 1981) are known from the Buck Creek drainage. *Notropis ariommus* was listed as of undetermined status but must be considered rare in Buck Creek, from which only 5 specimens are known. *Etheostoma cinereum* was listed as endangered and is known from only four drainages within the Cumberland river system of Kentucky, including Buck Creek (Burr 1980; Warren 1981). This large-stream and river darter prefers cover such as boulders, undercut banks, and rubble-gravel substrate mixed with detritus and/or *Justicia americana* in sluggish current adjacent to swift shoals (Saylor 1980; Warren 1981). Although the ashy darter has not been collected from Buck Creek since 1955, it may persist in suitable habitat along the mainstem between KY 80 and KY 192.

Three faunal units were discerned when the fish faunas of the 21 mainstem collecting sites were analyzed to determine average faunal resemblance (Table 3). The units were comprised by sites 1-27, 31-33, and 35-39, respectively, (hereinafter referred to as Units 1, 2, and 3) based on greater than 50% shared fauna. Divergence from this standard within each unit is attributed to sampling artifact.

The fauna of Unit 3 (Table 4) was characteristic of low-gradient habitats such as lakes, impoundments, and medium-to-large rivers (Pflieger 1975; Smith 1979; Trautman 1981) and was markedly different from that of the other units. Fifteen of the twenty-nine species collected from Unit 3 were limited in distribution to this section of Buck Creek.

Faunal differences were less pronounced between the two remaining units (Table 3). Sites 1-14 were faunistically similar to 21-27 but generally shared 40% or less of the fauna with Unit 2 (sites 31-33). Sites 21-27

Table 4. Species composition and longitudinal distribution of fishes at Buck Creek mainstem collection sites.

Species	Collection Sites																				
	1	2	3	4	10	12	14	21	22	23	24	25	27	31	32	33	35	36	37	38	39
Lepomis humilis	X																				
Catostomus commersoni		X																			
Etheostoma spectabile		X																			
Phoxinus erythrogaster				X																	
Ictalurus natalis				X																	
Rhinichthys atratulus	X			X																	
Semotilus atromaculatus	X	X		X	X			X		X	X										
Etheostoma flabellare	X	X	X		X	X	X	X		X	X										
Notropis ardens	X	X	X	X	X	X	X	X		X	X	X	X								
Lepomis cyanellus	X							X			X		X								
Etheostoma virgatum	X		X	X	X	X	X	X	X	X	X	X	X								
Notropis chrysocephalus	X	X	X	X	X	X	X	X		X			X		X						
Fundulus catenatus	X	X	X	X	X	X	X	X		X	X		X		X						
Etheostoma stigmaeum	X		X		X	X	X	X	X	X	X	X	X	X	X						
Pimephales notatus	X	X	X		X	X	X	X	X	X	X	X	X		X	X					
Hypentelium nigricans	X					X	X	X		X	X		X		X	X					
Etheostoma caeruleum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					
Campostoma oligolepis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	
Lepomis megalotis	X	X	X		X	X	X	X	X	X	X	X	X		X				X	X	
Micropterus dolomieui	X	X								X	X		X		X					X	
Lepomis macrochirus	X	X		X	X	X		X		X	X	X	X	X		X	X	X	X	X	X
Notropis telescopus		X	X		X	X	X			X	X	X	X		X						
Etheostoma blennioides		X	X		X			X		X	X	X	X	X	X	X					
Notropis boops			X							X	X										
Moxostoma duquesnei			X								X		X				X				
Notropis rubellus					X		X			X		X	X		X	X					
Percina caprodes					X				X	X	X	X	X	X	X	X		X	X		
Etheostoma camurum						X				X	X	X	X	X	X	X					
Ericymba buccata							X			X											
Ambloplites rupestris							X	X		X	X	X	X		X						
Notropis galacturus							X	X	X	X	X	X	X	X	X	X					
Etheostoma maculatum							X			X	X	X	X	X	X	X					
Percina maculata								X					X								

Noturus flavus								X		X	X	X			X						
Notropis ariommus								X							X	X					
Notropis spilopterus								X		X	X		X	X	X	X					
Notropis whipplei								X							X	X					
Moxostoma erythrurum								X	X	X	X		X			X					
Micropterus punctulatus								X	X	X	X		X	X	X			X	X	X	
Etheostoma cinereum									X				X								
Hybopsis amblops									X	X	X	X	X	X	X	X					
Ichthyomyzon bdellium										X	X		X		X						
Etheostoma zonale										X	X	X	X		X						
Labidesthes sicculus										X				X	X			X		X	
Cottus carolinae												X	X		X	X					
Notropis photogenis													X	X	X						
Hybopsis dissimilis													X		X	X					
Moxostoma macrolepidotum															X						
Notropis atherinoides															X	X		X			
Lepomis gulosus															X			X	X	X	
Micropterus salmoides															X					X	
Dorosoma cepedianum															X		X	X		X	X
Pomoxis annularis															X		X			X	X
Aplodinotus grunniens															X					X	X
Carpiodes cyprinus																	X			X	
Moxostoma carinatum																	X			X	
Ictalurus punctatus																	X			X	
Cyprinus carpio																	X			X	X
Notropis buchanani																		X	X		
Pimephales vigilax																			X		
Lepisosteus osseus																				X	
Carpiodes velifer																				X	
Ictiobus bubalus																				X	
Ictalurus furcatus																				X	
Pylodictis olivaris																				X	
Morone chrysops																				X	
Lepomis microlophus																				X	
Stizostedion vitreum																				X	
Dorosoma petenense																				X	X
Total species	17	15	14	11	16	14	17	24	12	32	30	20	33	14	36	19	8	8	7	24	6

generally shared 50% or more of the fauna with sites 31-33 and exhibited a gradual increase in similarity to these sites with each successively closer site. The transitional nature of the fauna of sites 21-27 relative to sites 1-14 and 31-33 is reflected by faunal resemblance values calculated by pooling the fauna of each group of sites. Sites 21-27 had 72% and 79% shared fauna with 1-14 and 32-33, respectively. Sites 1-14 and 31-33 had 49% shared fauna.

Analysis of the species characteristic of Units 1 and 2, based upon the occurrence of a species in greater than 50% of the sites comprising each unit, further illustrates the distinctions and similarities between the two units (Table 4). Species characteristic of Unit 1 included *Notropis ardens*, *N. chrysocephalus*, *N. telescopus*, *Semotilus atromaculatus*, *Fundulus catenatus*, *Etheostoma flabellare*, and *E. virgatum*. These are generally creek or small-stream fishes that migrate downstream in fall to overwinter in larger and deeper waters (Pflieger 1975; Smith 1979; Trautman 1981) such as that present in sites 21-27. *Hybopsis amblops*, *H. dissimilis*, *Notropis ariommus*, *N. atherinoides*, *N. photogenis*, *N. rubellus*, *N. spilopterus*, *N. whipplei*, *Labidesthes sicculus*, *Etheostoma camurum*, *E. maculatum*, and *Cottus carolinae* were characteristic of Unit 2 and typically inhabit moderate-to-large streams and small rivers (Pflieger 1975; Etnier 1976; Smith 1979; Trautman 1981). Elsewhere in Buck Creek these fishes were collected almost exclusively from the downstream portion of Unit 1, sites 21-27. This indicates that sites 21-27 supported a mixture of small-stream, large-stream, and small-river fishes and may be considered an area of transition between the faunas of Units 1 and 2. Several species were excluded from this analysis because they: (1) were collected from sites in all three units and were considered ubiquitous (*Campostoma oligolepis*, *Lepomis macrochirus*, *L. megalotis*, *Micropterus dolomieui*, and *Percina caprodes*), or (2) occurred extensively throughout Units 1 and 2 and were thus not useful in identifying differences between these units (*N. galacturus*, *Pimephales notatus*, *Hypentelium nigricans*, *Etheostoma blennioides*, *E. caeruleum*, and *E. stigmaeum*).

The pattern of longitudinal distribution of fishes along the Buck Creek mainstem was similar to that reported by Guillory (1982) for a Louisiana stream, and involved: (1) the addition of species in the middle section of Buck Creek (sites 21-33) to those widely distributed throughout sites 1-27, and (2) replacement of upper- and middle-river species with those typical of low-gradient, big-river habitat in the lower impounded section of Buck Creek (Table 4). A general downstream increase in the number of species was also noted (Table 4) and has been reported for other streams (Kuehne 1962; Larimore and Smith 1963; Sheldon 1968; Lotrich 1973; Guillory 1982). We believe that this pattern

would have been more distinct if an additional collection site in the intermittent headwaters of Buck Creek had been established, and through further sampling of deepwater habitat in the downstream section of Unit 2 and in Unit 3.

The faunas of each unit are a product of the diverse conditions found among the units. Numerous physicochemical factors that determine stream habitat diversity have been correlated with the longitudinal succession of stream fishes. These factors include, but are not limited to, depth (Sheldon 1968), drainage area (Larimore and Smith 1963), gradient (Trautman 1942; Burton and Odum 1945), pool size (Minckley 1963), stream order (Kuehne 1962; Lotrich 1973), and stream width (Burton and Odum 1945). Physicochemical factors excluded as primary causes of observed faunal differences between the upper and middle sections of Buck Creek included water quality, which Harker et al. (1979, 1980) reported as similar between the two areas, and substrate, which was characteristically cobble, slab boulder, and bedrock throughout the stream.

Observed faunal differences probably resulted from the interrelationship of numerous physicochemical factors as postulated by Guillory (1982). Since species characteristic of faunal Unit 1 of Buck Creek were also an important component of the Unit 2 fauna, the habitat requirements of additional species characteristic of Unit 2 may explain faunal differences (Table 4). These species (e.g., *N. atherinoides*, *N. photogenis*, *H. dissimilis*, *E. camurum*, *E. maculatum*) typically inhabit moderate-to-large streams and rivers and are thus adapted to relatively stable environments. We speculate that factors such as discharge and permanence of flow are important determinants of faunal differences observed between Units 1 and 2. These factors, which are more constant in the large-stream or small-river habitat of Unit 2 than Unit 1, are closely interrelated with several of the previously cited physicochemical factors, and are important to the maintenance of a stable environment.

The fauna of the lower impounded river was also related to the type of habitat present. Within this part of Buck Creek gradient is low and the stream is deep (10-25 m), providing habitat suitable for large-river and lentic species (Table 4).

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Paracricotopus millrockensis, a New Species of Orthocladiinae (Diptera: Chironomidae) from the Southeastern United States

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ABSTRACT.— The adult male and female, and immature stages, of *Paracricotopus millrockensis* n. sp. are described from specimens collected in Georgia and North Carolina. This species is also known from South Carolina. The new species is clearly separable from other species of *Paracricotopus* in the larval, pupal, and adult female stages. The male is very similar to *P. niger* (Kieff.). The immature stages of *P. millrockensis* have been found in small streams associated with stone substrates, and the larvae feed mainly on detritus and algae.

INTRODUCTION

Saether (1980a) revised and emended the generic diagnoses for all stages and both sexes of *Paracricotopus* Thienemann and Harnisch. In North America only one species of this genus has been described, *Paracricotopus glaber* Saether, from South Carolina. I collected in an urban Georgia stream specimens that, based on Saether's diagnoses, belong to *Paracricotopus*, but the pupal stage clearly differed in several characters from published descriptions of known species. This paper describes the new species and presents information concerning several aspects of its ecology and distribution.

The various life stages were obtained from specimens reared in isolation. All specimens were preserved in 70 percent ethanol prior to mounting on microscope slides. Some specimens were dissected, cleared, or fixed, and all were mounted in Euparal or Canada balsam.

In the following discussions, N= the number of specimens examined, and measurements are usually expressed as the total range. All measurements were made with a calibrated ocular micrometer. Except where otherwise noted, all measurements are given in μm. The numerals in parentheses indicate the number of features used to derive the range given. General terminology follows that of Saether (1980b).

Paracricotopus millrockensis n. sp.

Male.— N = 2; one specimen a mature pupa.

Head. Eyes pubescent, without dorsal elongation. Inner verticals

1-2 (4); outer verticals 2 (4); clypeal setae 6-10 (2). Lengths of palpal segments 2-5: 34 (2), 56 (2), 63 (2), 104-106 (2). Antennal ratio 0.62-0.63 (3); flagellomeres brown with darker brown pedicel.

Thorax. Light brown with brown vittae, preepisternum, scutellum, and postnotum. Antepronotum with 1-2 (4) lateral setae. About 5 short acrostichals present on anterior portion of scutum, beginning near antepronotum; 6-9 (4) dorsocentrals; 3 (4) prealars; about 4-6 (2) scutellars. Haltere very faintly brown with basal area darkest.

Wing. Length from arculus to tip 0.97 (2) mm, maximum width 0.32 (2) mm; V.R. of 0.93 (2); 3 (2) squamals.

Legs. Sensilla chaetica not evident at 500X. Lengths and proportions:

	fe	ti	ta_1	ta_2	ta_3
P_1	389-394(2)	389-418(2)	267(1)	209(1)	162(1)
P_2	371-377(2)	354-377(2)	162(1)	96(1)	75(1)
P_3	360-371(2)	412-417(2)	220(2)	125-128(2)	104-110(2)

	ta_4	ta_5	LR	SV	BV
P_1	104(1)	---	0.69(1)	2.91(1)	---
P_2	41(1)	49(1)	0.43(1)	4.65(1)	3.51(1)
P_3	52(2)	52(2)	0.53(2)	3.51-3.58(2)	3.03(2)

Abdomen. Pale brown. Tergites with anterior row of about 2-4 setae, and median row of about 5-7 setae. Hypopygium as shown in Figure 1. Anal point 17-26 (2) long with 2 or 3 setae on each side. Laterosternite IX apparently with 1 or 2 setae. Gonocoxite length 126 (4); gonostylus length 52-60 (4); apical spine of gonostylus 9 (4) long. Phallapodeme 46-49 (4) long; transverse sternapodeme 63-74 (2) long. H.R. of 2.10-2.42.

Female.— N = 3; one specimen a mature pupa. Similar to male except for the following differences.

Head. Inner verticals 2-3 (6); outer verticals 3 (6); clypeal setae 11-12 (2). Lengths of palpal segments 2-5: 31-34 (2), 57 (2), 60-63 (2), 109 (2). Antennal flagellomere lengths: 56-49 (6), 29 (6), 26-29 (6), 27-31 (6), 54-66 (5). Coronal suture absent.

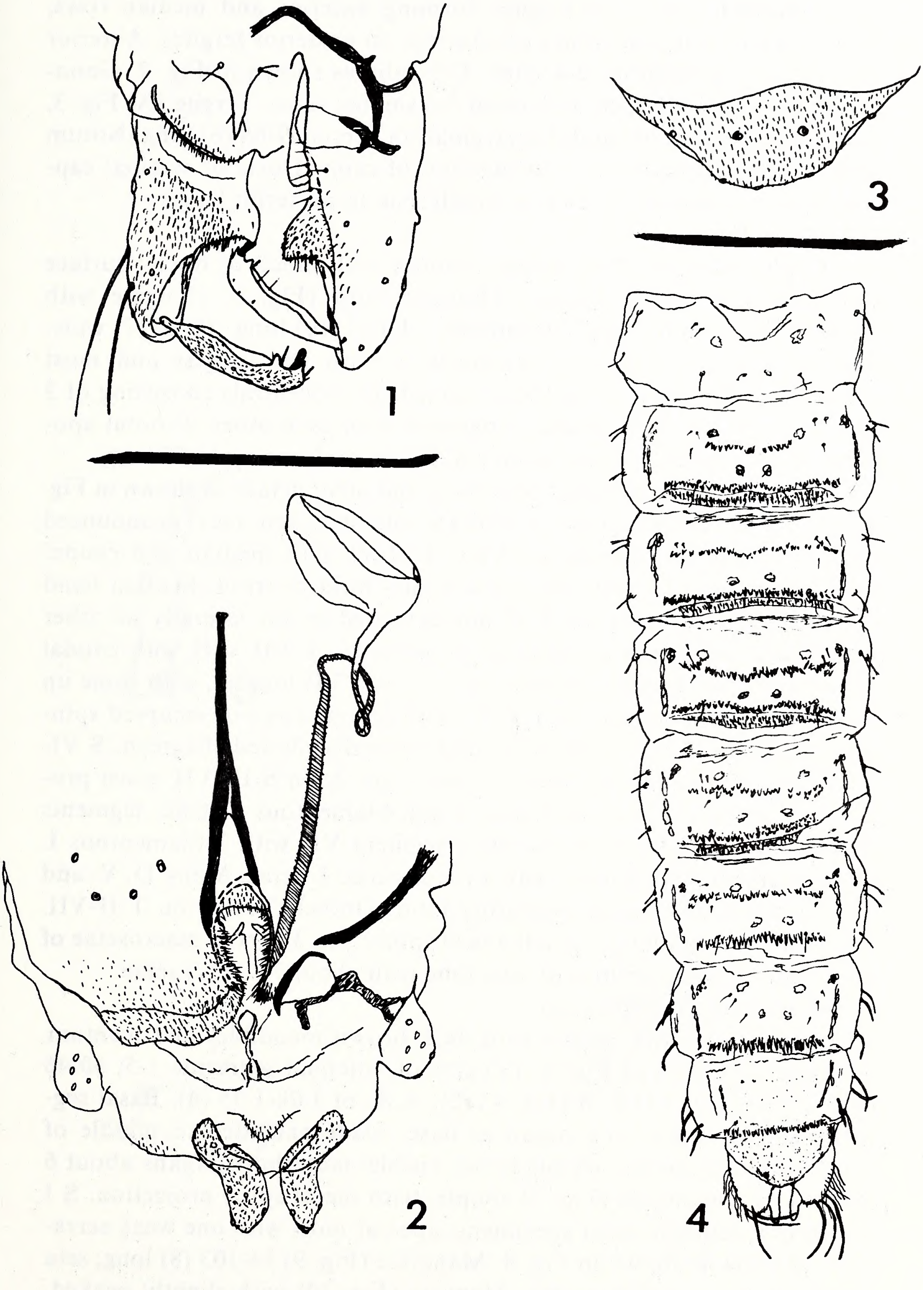
Thorax. 7-8 (3) acrostichals.

Wing. Length from arculus to tip 0.09-0.95 (4) mm; maximum width 0.36-0.39 (4) mm; 3-5 (4) squamals; V.R. of 0.92 (4).

Legs. 9 and 11 or 12 sensilla chaetica evident on ta_1 of p_2 and p_3, respectively. Lengths and proportions:

	fe	ti	ta_1	ta_2	ta_3
P_1	377-394(3)	389-435(4)	206-232(4)	145-157(4)	110-116(4)
P_2	336-377(4)	313-383(4)	139-157(4)	75-87(4)	64-67(4)
P_3	336-365(4)	383-406(4)	186-203(4)	99-110(4)	84-99(4)

	ta_4	ta_5	LR	SV	BV
P_1	64-81(4)	52-58(3)	0.52-0.57(4)	3.40-3.67(3)	2.55-2.56(2)
P_2	35-41(4)	44-52(4)	0.39-0.44(4)	4.67-5.09(4)	3.57-3.88(4)
P_3	44-46(3)	49-52(4)	0.49-0.50(4)	3.76-3.91(4)	3.15-3.20(3)



Figs. 1-4. *Paracricotopus millrockensis*, Male: 1, hypopygium, dorsal view to the left, ventral view with internal structure to the right; 2-3, Female: 2, genitalia, ventral view, with internal structure to the right; 3, T IX, dorsal view; Pupa: 4, abdominal tergites and anal end.

Abdomen. Setae on tergites forming anterior and median rows, though separation sometimes not distinct on posterior tergites. Anterior row consisting of about 2-4 setae. Genitalia as shown in Fig. 2. Gonocoxite IX with 3-4 larger, and about 3-5 smaller setae. Tergite IX, Fig. 3, without indication of caudal emargination. Cerci 57-66 (6) long. Notum with a light triangular area at junction of rami. Ducts of seminal capsules much narrower in anterior length than in posterior length.

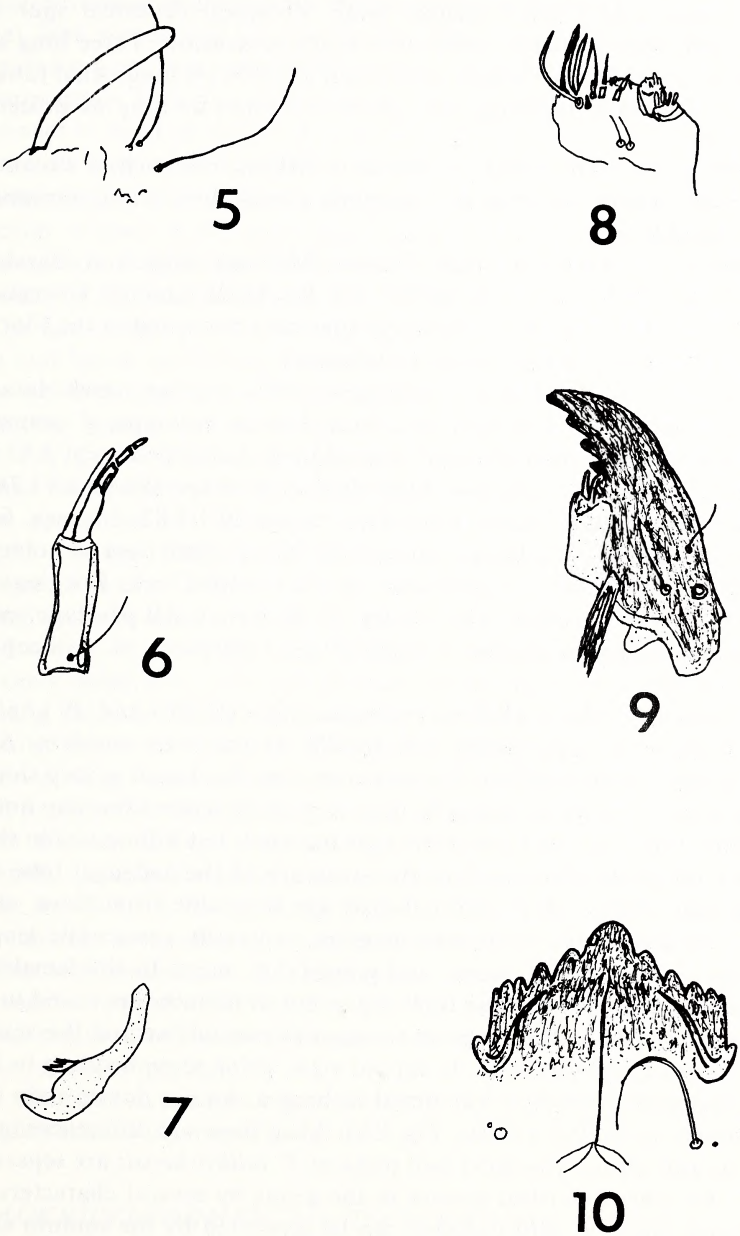
Pupa.— N = 6.

Cephalothorax. Pale brown. Thorax with much of dorsal surface reticulate and faintly rugose. Thoracic horn (Fig. 5) elongate with rounded apex, entire surface smooth, 74-157 (10) long, 10-20 (7) wide. Median antepronotals 2; precorneals 3, with Pc_2 longest and most robust, and Pc_3 shortest and least robust. Dorsocentrals consisting of 2 pair with Dc_1 and Dc_2 widely separated from each other. Frontal apotome slightly to moderately wrinkled; FS on prefrons up to 57 long.

Abdomen. Pale brown. Chaetotaxy and other details as shown in Fig. 4. T I-VII without shagreen. T VIII-IX with shagreen, most pronounced on T IX, and very sparse on VIII. T II-VI with median and caudal bands of spines and spinules; a few spines bifid or trifid. Median band of spines and spinules on T II not extended as far laterally as other bands, and may appear interrupted medially. T VII-VIII with caudal spines and spinules only. Spines on T VI and VII longest, with some up to 23 long. Conjunctives of T II-VI with several rows of recurved spinules. Sternites II-VIII with faint, uniformly distributed shagreen. S VI-VII with a few caudal spinules. Pedes spurii A on S IV-VII, most pronounced on S VI. Segment I with 2 non-filamentous L setae, segments II-VI with 3 non-filamentous setae, segment VII with 3 filamentous L setae, segment VIII usually with 4 filamentous L setae. Many D, V, and non-filamentous L setae appearing bifid. Dorsal O setae on T II-VII. Anal lobe with about 2-4 small apical spines and 3 curved macrosetae of about equal length. Fringe of anal lobe with about 7-12 (12) setae.

Larva.— N = 9; final instar.

Head. Yellowish brown with dark brown mandibles and mentum. Antenna as shown in Fig. 6. Lengths of antennal segments 1-5; 40-46 (12), 17-20 (12), 7 (12), 6 (12), 4 (12); A.R. of 1.08-1.35 (4). Basal segment 17 (11) wide; ring organ at base; blade extended to middle of fourth segment; accessory blade not visible; lauterborn organs about 6 (6) long. Premandible (Fig. 7) simple, with mesal spiny projection. S I appearing simple in most specimens, apex at most with one weak serration. Maxilla as shown in Fig. 8. Mandible (Fig. 9) 94-103 (8) long; seta interna with several branches. Mentum (Fig. 10) with slightly peaked, but generally rounded median tooth 19-20 (4) wide; median tooth sometimes weakly notched on each side; fifth lateral tooth small. Ventromental plates about 2-3 (8) wide. Width of ventromental plate/width of median tooth 0.10-0.16. Postmentum 126-134 (8) long.



Figs. 5-10. *Paracricotopus millrockensis*, Pupa: 5, thoracic horn and precorneal setae; 6-10, Larva: 6, antenna; 7, premandible; 8, maxilla, ventral view; 9, mandible; 10, mentum and postmental area.

Abdomen. Procerci dark brown, up to 26 long, 17 wide, with a basal curved spur and 2 short median setae. Preapical procercal spur not developed, represented at most by a slight protrusion. Three long and two shorter anal setae; longest seta about 450-500 (3) long. Anal tubules slender, gradually tapering, and about 2.5 times as long as posterior parapods.

Etymology.— The species is found in Millrock Branch, a stream in Rockdale County, Georgia, that supports a most diverse and interesting chironomid fauna.

Holotype.— Reared ♂, with exuviae, Millrock Branch at Haralson Mill Road (83°57′24″ N, 30°45′41″ W), Rockdale County, Georgia, 3 VII 83, leg. B. A. Caldwell. Holotype specimen deposited in the Florida State Collection of Arthropods (Tallahassee).

Paratypes (9).— Reared ♀ (allotype), with exuviae, same data as holotype; reared ♀, with exuviae, same data as holotype; ♂ prepared from mature pupa, with exuviae, same data as holotype except 3 VI 82; mature ♀ pupa, with exuvium, same data as holotype except 2 VI 78; ♀ pupal exuvium, same data as holotype except 20 III 82; 2 larvae, final instar, same data as holotype; larva, final instar, same data as holotype except 19 VII 77; larva, final instar, Huffines Mill Creek, Rockingham County, North Carolina, VIII 81, leg. D. R. Lenat. All paratype specimens are deposited in the Florida State Collection of Arthropods (Tallahassee).

Diagnosis.— Males of *Paracricotopus niger* (Kieff.) and *P. uliginosus* (Brund.) are very similar structurally, as has been noted by Albu (1968) and Saether (1980a). *Paracricotopus millrockensis* is very similar to these two species structurally, and consistent separation may not be possible. I have not borrowed the type material, but differences in these species might be discovered in the structure of the aedeagal lobe and gonostylus. Males of *P. millrockensis* are separable from those of *P. glaber* by differences in the hypopygium, especially gonocoxite length, aedeagal lobe size and shape, and gonostylus shape. In the female, *P. millrockensis* is most similar to *P. niger*, but differences are found in the genitalia, especially the shape of the coxosternapodeme and the ventral lobe of gonopophysis VIII. In lateral view, prior to embedding in balsam, the allotype female was noted to have a thinner notum than that illustrated by Saether (1980a, Fig. 2A). Also, there are differences in leg lengths and ratios. The larva and pupa of *P. millrockensis* are separable from the other described species in the genus by several characters. In the pupal stage, *P. millrockensis* can be separated by the smooth elongate thoracic horn, different abdominal chaetotaxy, and different anal lobe. Its anal lobe is very similar to that of *P. niger*, based upon the figure of Thienemann (1950). Saether (1980a), however, reported 8-15

apical spines with an average of 10 in specimens that he examined. *Paracricotopus millrockensis* differs from *P. glaber* in having apical anal lobe spines and an anal fringe. The larva of *P. millrockensis* is separable from these other species by the apparently simple S I, shorter postmentum, lack of a developed pre-apical procercal spur, minor differences in mentum structure, and the anal tubules, which are about 2.5 times as long as the posterior parapods. Other characters that may further separate *P. millrockensis* from the structurally similar *P. niger* include a lower A.R., more posterior position of the submental setae, and apparent differences in the shape and size of the anterior lacinial chaetae of the maxilla (cf. Saether 1980a:138).

Range.— *Paracricotopus millrockensis* has been collected in Georgia and North and South Carolina. The preferred habitat appears to be low order streams in the Piedmont and Blue Ridge Provinces. In Georgia, this species has been collected in Cascade Branch, Habersham County, and in Millrock Branch, Rockdale County. In South Carolina, it has been collected in Boone Creek, Oconee County. In North Carolina, specimens of this species have been collected in Beaverdam Creek, Wake County, Huffines Mill Creek, Rockingham County, and in an unnamed stream, Macon County. The species is likely to occur in similar streams in other southeastern states.

Ecology.— In North and South Carolina streams, and Georgia streams other than Millrock Branch, larvae have been collected from among stone substrates in qualitative samples. In the Georgia stream locally known as Millrock Branch, the species has been collected by hand-picking from very shallow water on granitic bedrock among moss and detritus. In this stream, most larvae have been found in association with *Hudsonimyia parrishi* Caldwell and Soponis. Some other chironomids found in the same microhabitat, but not necessarily at the same time, are listed in Caldwell and Soponis (1982). Millrock Branch drains a relatively undeveloped, unpolluted watershed with dissolved oxygen values near saturation. D. Lenat (pers. comm.), however, has collected larvae in some North Carolina streams influenced by pesticides and other pollutants. This would suggest that the species is not a good indicator of water quality.

Detritus, fungi, and algae constitute the majority of food observed in gut contents of several larvae.

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Aquatic Distributional Patterns in the Interior Low Plateau

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ABSTRACT.— The aquatic gastropod and fish faunas of the Interior Low Plateau of extreme southern Indiana, Illinois (Wabash River drainage), Kentucky, Tennessee, and northern Alabama reflect the interaction of tectonic changes, glaciation, eustatic stream modifications, piracy within the Low Plateau and in extralimital drainages (particularly the Coosa-Alabama system), immigration from trans-Mississippian systems, speciation within drainages that cross the Low Plateau, and survivorship as relicts. Examples in the Pleuroceridae, Unionidae, and several fish families are discussed, with emphasis on percid darters and the catfish genus *Noturus*.

INTRODUCTION

The Interior Low Plateau of extreme southern Indiana, Illinois (Wabash River drainage), Kentucky, Tennessee, and northern Alabama (Fenneman 1938; Quarterman and Powell 1978) is a biological crossroads between regions that are faunistically and floristically rich. Understanding of the biological importance of this unique region has come very slowly, piecemeal really, mostly because of inadequate study and failure in the synthesis of existing information. The present biota is quite complex, consisting of mixtures of types from diverse centers of origin, including a rather large number of relicts and endemics. To extrapolate from knowledge of existing biotas back into the past in order to understand the present is not a bad approach, particularly if there are considerable supporting geologic and paleontologic data available.

MOLLUSCA

In the discussion that follows, I have elected to retain Goodrich's nomenclature (see literature cited) rather than the combinations recently espoused by Burch (1982), since most readers are not familiar with the resurrected combinations. Furthermore, there is still considerable disagreement regarding some of the combinations.

In the early part of this century, well-diggers near Henderson, Kentucky, cut into a deposit 25.5 m below the surface. The strata were determined to be of Yarmouthian Interglacial age (Baker 1920). The mollusks removed from those deposits included specimens of *Campeloma crassula* Rafinesque, *Pleurocera canaliculatum* (Say), *Planorbula*

(*Menetus*) *dilatatus* (Gould), and *Valvata* species. The Yarmouthian followed the Kansan glacial epoch and was the longest interglacial. During that period the climate was slightly warmer than at present (Fenneman 1938), allowing many species to extend their ranges (Baker 1920). Later investigations of Yarmouthian deposits near Evansville, Indiana (Baker 1920), disclosed the presence of unionid clams and various snails that no longer live in streams of the Interior Low Plateau. For example, *Quadrula quadrula asper* (Lea 1831) now lives in streams that drain into the Gulf of Mexico from Alabama to central Texas and northward to Kansas. Another species with derivatives still present in many Low Plateau streams, *Amblema plicata* Say, has its principal and parental stocks distributed from the Alabama River drainage and streams flowing into the Gulf of Mexico west to central Texas and north to central Kansas. Three additonal operculated snails were found in the well deposits: *Pleurocera unciale* (Haldeman), *P. alveare* (Conrad), and a species of *Lioplax*. The last two still live in the Ohio River and many of its tributaries, whereas the first is now restricted to the upper tributaries of the Tennessee River in Virginia and eastern Tennessee (Burch 1982; Goodrich 1940); all have their principal relatives in the Alabama River system.

Many deposits of the previous Aftonian Interglacial and the Illinoian glacial period (Browne and Bruder 1963) indicate climatic conditions that were considerably cooler and moister than at present. Ice movement, completely overwhelming stream systems to the north, caused a southward shift of faunas and, upon recession, a re-expansion northward. Thus, many of the species found themselves exposed to new environmental and competitive conditions that perhaps stimulated extensive differentiation into species and races in extralimital areas. Many gastropod species that are now restricted to more northerly latitudes occurred in the Interior Low Plateau during Pleistocene times (Browne and Bruder 1963) although some derivative species remain. They include *Amnicola*, various species of *Lymnaea*, and *Helisoma anceps* (Menke) (Branson 1972).

The presence of the Alabama and Tennessee river system derivatives in Interior Low Plateau streams, as far north as the Wabash River of Indiana and Illinois, raises questions regarding migratory pathways and strengthens a theory previously in vogue. Baker (1920) postulated existence of an Appalachian river that included parts of the old Teays and Tennessee rivers and their tributaries above Chattanooga and the Coosa-Alabama system. Whether it is necessary to invoke the existence of such a river is open to debate; other mechanisms can explain the observed distributions. However, that the Alabama River system, in particular the Coosa basin, has been a potent generator of species is

scarcely open to argument. The Coosa River had more endemic species of operculated gastropods than any other river in North America (Goodrich 1944a), including members of the families Pleuroceridae and Viviparidae. Two of eleven species of *Somatogyrus* that occur in the Coosa also live in the Tennessee River, and *Goniobasis carinifera* (Lamarck) lives in both drainages (Goodrich 1944a).

A very characteristic pleurocerid genus of the Alabama-Coosa system is *Anculosa* (*Leptoxis*, according to Burch 1982), which has a large number of endemic species not found outside that system but also has derivatives that occur elsewhere (Goodrich 1922). Some of these species occur in Low Plateau drainages, including the related genus *Nitocris* (Branson 1972). *Nitocris* (relegated to *Mudalia* by Burch 1982) has been able to extend its range into the Kanawha of West Virginia, the Hiwassee of North Carolina, the Tennessee River, and the Ohio and Little Miami of Ohio, Indiana and Kentucky (Goodrich 1940, 1944a). Alabama River derivatives of *Anculosa* occur in the Tennessee, Cumberland and Green rivers (Burch 1982; Goodrich 1934). *Anculosa subglobosa* Say lives in the Cumberland River system of central Tennessee (Goodrich 1921). *Anculosa praerosa* Say, a secondary Tennessee River system derivation, occurs in the Tennessee system; in the Cumberland, Holston, Duck, Clinch, Little Tennessee, and Obey rivers of Tennessee; in tributaries of the Duck and Tennessee rivers in Alabama (Burch 1982; Goodrich 1944b; TVA 1975); and in the Blue and Wabash rivers of Indiana. Thus, it is clear that streams of the Interior Low Plateau have served as important migration pathways into the Ridge and Valley Province and elsewhere.

There are many endemic pleurocerid species in the Tennessee and Cumberland river systems (Goodrich 1940). *Pleurocera prasinatum* (Conrad) of the Alabama River system is most closely related to *P. canaliculatum* (Say) (Goodrich 1935), various forms of which occur in the Tennessee, Cumberland, Clinch, Kentucky and Ohio rivers. It has also been able to penetrate into the Wabash of Indiana (Goodrich 1929), doubtless via the Ohio since the ancestral Wabash of Indiana and Illinois was almost completely overwhelmed during Wisconsin glaciation. *Lithasia obovata* (Say) and *L. geniculata* Haldeman are both considered Tennessee River derivatives. *Lithasia geniculata* is relatively widespread in the Interior Low Plateau of the Tennessee River in Tennessee (Burch 1982). It was recently discovered in the southwestern section of the Kentucky portion of the Low Plateau (Branson et al. 1983), and is common in parts of the lower Tennesse (TVA 1975). *Lithasia obovata* had spread from the Tennessee River basin into the Green, Cumberland and Kentucky river basins and, via the Ohio River, into the Wabash of Indiana and the Scioto of Ohio (Goodrich 1929).

Goniobasis laqueata (Say), common in the Tennessee River basin (TVA 1975) and Cumberland River (Branson and Batch 1982), is another species that has spread into various segments of the Interior Low Plateau drainages from the Tennessee basin. *Goniobasis semicarinata* has its center of distribution in the Kentucky River drainage (Branson and Batch 1981). It entered the Cumberland River (Branson and Batch 1982), possibly by stream capture such as that documented by Kuehne and Bailey (1961), and the Salt River of Kentucky and the Wabash of Indiana (Goodrich 1935), perhaps by tributary hopping and reinvasion.

Many additional examples in the Pleuroceridae and Unionidae illustrate the principles involved, but the ones presented here shall suffice. From the very rich centers of endemicity in the Alabama-Coosa system and secondary speciation centers in the Tennessee and Middle Cumberland systems, the Pleuroceridae and Viviparidae (*Somatogyrus*, *Viviparus*, *Campeloma*) expanded northward and westward into the Cumberland, Green and Lower Tennessee rivers, and via them into the Ohio River basin. Depauperacy is one of the main features in the northern part of the area. The Tennessee and Cumberland rivers served as major refugia for unionid species that later reinvaded upstream Ohioan streams, and the Green River may have served as a refugium as well. All three rivers were sources for repopulation of the Wabash and Maumee rivers in postglacial times (Johnson 1980). Pleurocerids were able to reinvade Ohio and Indiana from similar sources via the Ohio River, penetrating into the Wabash River and its tributaries. Or perhaps, as discussed below, they came from some of the other old tributaries of the Teays system.

FISHES

Fish and mollusk distributional patterns in the Interior Low Plateau must be correlated with various physical and hydrologic phenomena in order to account for observed faunal relationships between drainage basins. According to Lachner and Jenkins (1971), there are four principal ways that aquatic organisms have achieved or may achieve new dispersal distributions: (a) stream capture, (b) eustatic changes in coastal plains, (c) Pleistocene modifications of drainages, and (d) movements from one drainage to another via past and existing interconnecting main streams. These mechanisms were perhaps involved in structuring the fauna of the Interior Low Plateau. Pleistocene glaciation certainly affected the region, very obviously so in the Shawnee Hills, the northern boundary of which (38th parallel) is demarked by glacial till (Harker et al. 1980, and literature cited therein). In this same general area, numerous karsts and faults crisscross the Green, Pond, Tradewater, Rough, Barren, and Ohio rivers.

To the west and southwest the Plateau is separated from the Coastal Plain Province by the Tennessee and Cumberland rivers in Kentucky, except along a narrow isthmus that abuts Missouri after crossing extreme southern Illinois, and by the Tennessee River in Tennessee and northwestern Alabama. The whole plateau is an ecotonal region, past and present, that lies in the western mesophytic forests, although slender extensions of the southeastern forests penetrate along rivers. The narrow connection between the Ozark Plateau and the Low Plateau through Indiana and Illinois has exerted an important influence on the floras and faunas, both east and west (Conant 1960).

In postglacial times, particularly during the so-called Climatic Optimum, the mesic forest and its streams, many of which are now buried (Wayne 1952), were apparently much more extensive than at present. They extended well up into the glaciated parts of Ohio, Indiana and Illinois. During the Xerothermic period that followed, the mesic forest vanished from most of the area above the Ohio River (Conant 1960), forcing a shrinkage in ranges of many organisms and leaving many of them in the narrow isthmus, an area thought to have been stable along the upper margin of the Mississippian Embayment since at least Tertiary times. Conant (1960) believed that many organisms used this narrow isthmus to extend their ranges east and west, including various species of *Eurycea*, *Plethodon*, and *Natrix*, and the fishes *Hybopsis dissimilis* (Kirtland), *Noturus eleutherus* (Jordan), and *Notropis galacturus* (Cope). *Etheostoma microperca* Jordan and Gilbert, certain species of the percid subgenus *Nothonotus*, and *Notropis telescopus* (Cope) may have been involved in such exchanges as well. However, Pflieger (1971) noted that the hill country around the head of the Mississippi Embayment may have played a role in various eustatic changes that allowed fish exchanges through the Embayment rather than around it via streams now absent.

Older geologic changes doubtless played a role in determining various aspects of the Interior Low Plateau's fauna, particularly pre-Cretaceous and Cretaceous Appalachian peneplanation (Griswold 1895, and others). One portion of such peneplains has been mapped westward through the Mississippi Embayment into Arkansas and northern Alabama, an important fact considering the putative sources of many Low Plateau organisms. Not only is the ancestral Cumberland River supposed to have crossed the northwestern Alabama axis, but there is a possibility that a Lower Mississippi stream, working backward from the embayment, captured much of the interior drainage from the old Teays system (Griswold 1895), transferring many aquatic species with it. Later events would have been of greater importance.

The Teays and the Old Ohio rivers greatly influenced the distribution of fishes and other aquatic organisms in the Low Plateau. According to Hocutt (1979), the Old Ohio River headed near the present confluences of the Salt River (Kentucky) and the Blue River (Indiana), a major tributary being the Green River from Tennessee and Kentucky. The Teays headed in North Carolina and flowed through Ohio, Indiana, and Illinois, then southward into the Mississippi Embayment; its major southern tributaries were the Old Kentucky and Old Licking rivers (Hocutt et al. 1978). Pleistocene glaciation destroyed most of the Lower Teays, creating the vast Upper Ohio River by westward diversion of the Big Sandy, Little Sandy, Licking, Kentucky, and Kanawha rivers and, during Kansan times (Wayne 1952), by diverting a large segment of the Teays system into the Wabash River. Such drainage modifications allowed eastern fishes, such as *Percina macrocephala* (Cope) and *Etheostoma blennioides blennioides* Rafinesque, to disperse westward into Low Plateau streams. This may account for the strong resemblances between the fish faunas of the Green and Licking rivers (Retzer et al. 1983) and the distribution of *Percina cymatotaenia* (Gilbert and Meek) and its undescribed sibling species (Branson and Batch 1974).

Lachner and Jenkins (1971) considered the Teays River to have functioned as a generation center, a reservoir of species, and a dispersal pathway. According to them, for example, the ancestral stock of *Nocomis micropogon* (Cope) evolved in the Upper Teays (Kanawha-New) system, and dispersed from there into the Lower Teays and into the southwestern Ohio basin. Since the Wabash was nearly completely overwhelmed by Pleistocene ice, the population in that stream has to be the result of later re-invasion from refugia to the south. Lachner and Jenkins (1971) presented evidence that *N. micropogon* entered the Tennessee River via stream capture, probably by headwater piracies between the Tennessee, Chattahoochee and Savannah rivers (Ross 1971). Ross (1971) also documented transfers of the Duck and Elk rivers from the Cumberland to the Tennessee and stream captures between the Coosa-Hiwassee and Tennessee rivers in northern Alabama. A Cumberland-Kentucky river drainage exchange of *Etheostoma sagitta* (Jordan and Swain), and doubtless other fishes as well, including *N. micropogon* (the only *Nocomis* in most of the Kentucky River), was documented by Kuehne and Baily (1961). If true, these exchanges would explain many of the mollusk and fish distributional patterns mentioned previously and below, and would strengthen the idea that the Tennessee, Coosa-Alabama , and Cumberland rivers have been potent differentiation and dispersal centers for various piscine, molluscan, and other groups of aquatic organisms.

There appears to have been considerable faunal exchange between the Alabama River system and the Mobile basin and the Tennessee River. The Tennessee and Alabama river systems share many species of

fishes (Table 1), and the Mobile and Escambia drainages share at least seven species: *Hybognathus hayi* Jordan, *Pimephales notatus* (Rafinesque), *Notropis baileyi* Suttkus and Raney, *Etheostoma histrio* Jordan and Gilbert, *E. proeliare* (Hay), *Percina ouachitae* (Jordan and Gilbert) (=*P. uranidea* (Jordan and Gilbert)), and *Stizostedion vitreum* (Mitchill) (Lee et al. 1980; Smith-Vaniz 1968). Many of these species, of course, range over much of the Low Plateau, although some of them are more restricted in distribution and some species have been unable to effect exchange between the river systems. *Etheostoma squamiceps* Jordan, for example, occurs in southern Illinois, western Kentucky, and southwestern Indiana (Wabash drainage in Posey County), and in the Tennessee River system of west-cental Tennessee, Alabama, and Mississippi (Page et al. 1976), but has not been reported from the Alabama River system. Many *Nothonotus* and *Catonotus* show similar distributional patterns, albeit superimposed upon strong endemicity.

The Tennessee, Cumberland and Green river systems have received varying contributions to their fish faunas from other systems, and have made contributions to other drainages in the Interior Low Plateau. All have served as piscine speciation centers and as reservoirs for endemic species. One of the sources for Low Plateau fishes was obviously the Lower Mississippi River system, but the species derived from there mostly exhibit marginal or extralimital patterns in the Plateau. Exceptions are seen in the Green and Tradewater rivers, Kentucky, where they have effected rather wide distribution. Elsewhere, these fishes retain populations in more or less stable, protected, relict habitats, like those reported by Gunning and Lewis (1955) in southwestern Illinois. The species assemblage of that swampine environment includes fishes with mostly southern affinities: *Aphredoderus sayanus* (Gilliams), common in the Green River; *Umbra limi* (Kirtland); *Fundulus notti* (Agassiz); *Elassoma zonatum* Jordan, historically common in both the Green and Tradewater rivers; *Lepomis symmetricus* Forbes; *Centrarchus macropterus* (Lacépède), common in the Green River; *Etheostoma gracile* (Girard), common in the Green River; and *Chologaster agassizi* Putnam, not southern but Low Plateau. *Umbra limi*, which also occurs sporadically along the margin of the Low Plateau (Clay 1975; Sisk 1973), is of northern origin. According to Wiley (1977), the *Fundulus notti* species complex originated in the Lower Mississippi basin and, abetted by stream captures between the Mississippi and the Mobile Bay drainages, spread elsewhere. *Fundulus notti* barely penetrates southwestern Kentucky (Burr 1980) and Tennessee (Baker 1939) outside the Low Plateau. In Tennessee, the only non-embayment record for *F. notti* is from the Big Sandy River, a system with a host of embayment species, although the species is widespread in the Obion, Forked Deer and Hatchie rivers (D. Etnier, pers. comm.).

A large percentage of the fishes in southern Indiana and adjacent Illinois and Kentucky are of southern or lowland origin, many of them doubtless gaining entry in post-glacial times by migration through the Ohio River and its tributaries. Illinois, for example, has two species complexes that are coincidental with the Mississippi and Ohio river drainages, respectively (Forbes 1909; Smith 1979), entering the area via the Wabash and smaller Ohio River tributaries. Included in this list are: *Ichthyomyzon bdellium* (Jordan), *Lampetra aepyptera* (Abbott), *Notropis atherinoides* Rafinesque, *N. fumeus* Evermann, *N. shumardi* (Girard), *N. venustus* (Girard), *N. volucellus* (Cope), *Ericymba buccata* Cope, *Nocomis micropogon* (Cope), *Hybopsis amblops* (Rafinesque), *H. gracilis* (Richardson), *H. meeki* Jordan and Evermann, *Noturus flavus* Rafinesque, *N. miurus* Jordan, *N. eleutherus* Jordan, *N. stigmosus* Taylor, *Fundulus olivaceus* (Storer), *Aphredoderus sayanus* (Gilliams), *Lepomis megalotis* (Rafinesque), *Centrarchus macropterus* (Lacépède), *Micropterus punctulatus* (Rafinesque), *Elassoma zonatum* Jordan, *Ammocrypta pellucida* (Putnam), *Percina ouachitae* (Jordan and Gilbert), *Etheostoma blennioides* Rafinesque, *E. fusiforme* (Girard), *E. histrio* (Jordan and Gilbert), *E. kennicotti* (Putnam), *E. proeliare* (Hay), and *E. squamiceps* Jordan. Properly speaking, *Etheostoma proeliare* is a fish of the Coastal Plains and Mississippi Embayment (Burr and Page 1978), as is *E. fusiforme* (Sisk 1973), and the distributional center of the subgenus *Ammocrypta* appears to have been in the Lower Mississippi basin (Williams 1975). In the Low Plateau region, *A. pellucida* is the most widespread member, but *A. clara* Jordan and Meek is known from the Green River in Kentucky. *Fundulus chrysotus* (Günther), *Notropis maculatus* (Hay), and *Menidia beryllina* (Cope) are all distinctive Gulf Coastal Plains fishes that barely impinge upon the Low Plateau in Kentucky without actually penetrating its drainages (Sisk 1973; Baker 1939; Burr and Mayden 1979).

As stated previously, in Kentucky the Land Between the Lakes region (Lower Tennessee-Lower Cumberland rivers) separates the Low Plateau from the Gulf Coastal Plains. The mix of fishes in this area reflects the various centers of origin; some examples are presented in Table 2 (McDonough 1974; Resh et al. 1972). A similar picture is presented by a partial list of fishes from Reelfoot Lake (Table 3), which barely laps northward into Kentucky (Parker 1939; Baker 1939). Some of the fishes in this area and elsewhere in the Low Plateau gained access to the region from the north, possibly via a temporary post-Wisconsin connection between the Erie and Wabash drainages, and Indiana's White and Big Blue drainages (Gerking 1945). They include *Umbra limi* (Kirtland), *Rhinichthys atratulus* (Hermann), *Percopsis omiscomaycus* (Walbaum), and *Fundulus catenatus* (Storer). Jordan (1877) reported

Table 1. Fishes shared by the Tennessee and Alabama River systems (Lee et al. 1980; Smith-Vaniz 1968).

Ichthyomyzon castaneus	*Ictiobus bubalus*
Ichthyomyzon gagei	*Ictiobus cyprinellus*
Lampetra aepyptera	*Minytrema melanops*
Amia calva	*Moxostoma carinatum*
Acipenser fulvescens	*Moxostoma duquesnei*
Scaphirhynchus platorhynchus	*Moxostoma erythrurum*
Polyodon spathula	*Moxostoma macrolepidotum*
Lepisosteus oculatus	*Ictalurus furcatus*
Lepisosteus osseus	*Ictalurus melas*
Anguilla rostrata	*Ictalurus natalis*
Alosa chrysochloris	*Ictalurus nebulosus*
Alosa alabamae	*Ictalurus punctulatus*
Dorosoma cepedianum	*Noturus gyrinus*
Hiodon tergisus	*Pylodictis olivaris*
Esox americanus	*Fundulus olivaceus*
Esox niger	*Gambusia affinis*
Campostoma anomalum	*Labidesthes sicculus*
Hybognathus hayi	*Morone chrysops*
Hybognathus nuchalis	*Morone mississippensis*
Hybopsis storeriana	*Ambloplites rupestris*
Nocomis leptocephalus	*Lepomis cyanellus*
Nocomis micropogon	*Lepomis gulosus*
Notemigonus crysoleucas	*Lepomis humilis*
Notropis atherinoides	*Lepomis macrochirus*
Notropis baileyi	*Lepomis megalotis*
Notropis bellus	*Lepomis microlophus*
Notropis chrysocephalus	*Micropterus punctulatus*
Notropis lirus	*Micropterus salmoides*
Notropis venustus	*Pomoxis annularis*
Notropis volucellus	*Pomoxis nigromaculatus*
Notropis whipplei	*Stizostedion vitreum*
Opsopoeodus emiliae	*Percina caprodes*
Pimephales notatus	*Percina maculatum*
Pimephales vigilax	*Percina ouachitae*
Rhinichthys atratulus	*Percina shumardi*
Semotilus atromaculatus	*Etheostoma nigrum*
Carpiodes cyprinus	*Etheostoma stigmaeum*
Cycleptus elongatus	*Cottus carolinae*
Erimyzon oblongus	*Aplodinotus grunniens*

Etheostoma camurum (Cope), *E. variatum* Kirtland, *E. spectabile* (Agassiz), *Ammocrypta pellucida* (Putnam), and *Percina copelandi* (Jordan) from the White River in Indiana, as well as the minnows *Hybopsis dissimilis* (Kirtland) and *Notropis ariommus* (Cope), and the sucker *Erimyzon oblongus* (Mitchill), most of these doubtless re-invading during post-glacial times via the Ohio River. The Wabash River, however, has been the principal Low Plateau pathway of piscine re-invasion into Indiana and Illinois (Table 4).

At least one species in this area, *Clinostomus funduloides* Girard, reported from the Lower Tennessee (Miller 1978), Cumberland (Burr 1980), and Little Sandy rivers and several other streams in northeast Kentucky (Bauer and Branson 1979), the Wabash drainage in Indiana (Lee et al. 1980; Gerking 1945; Blatchley 1938), and the Barren and Green rivers (Retzer et al. 1983), has a strongly pre-glacial relict distribution. This may be true also of *Rhinichthys atratulus.*

Fishes considered by Etnier (unpublished) to have strong lowland and Lower Mississippi affinities are presented in Table 5. In addition, he believes that several species of Low Plateau fishes are derivable from areas west of the Mississippi, from the Ozarkian and Great Plains faunal regions: *Hybopsis gracilis* (Richardson), *H. storeriana* (Kirtland), *Hybognathus hayi* Jordan, *H. nuchalis* Agassiz, *H. placitus* Girard, *Notropis lutrensis* (Baird and Girard), *N. camurus* (Jordan and Meek), *N. umbratilis* (Girard), *N. fumeus* Evermann, and *N. stramineus* (Cope). Such faunal exchanges could have occurred either via the aforementioned isthmus across southern Illinois and Indiana, or via the Mississippi-Ohio system. To this list should be added the percid subgenus *Nothonotus* (Zorach 1972; Harker et al. 1980) (see discussion below).

Although many fish species enjoy wide distribution throughout the Low Plateau, many others are restricted to certain portions of the area. One of the most interesting of such patterned distributions is endemicity, important in biogeographic studies and presenting several implications. Applied specifically to the Interior Low Plateau aquatic problem, endemicity may reflect interrupted gene flow imposed by isolation resulting from drainage modification and control (cut off from surrounding drainages) by master rivers like the Green (Kuehne 1966) and extralimital origins, dispersal into other drainages and modification and divergence in the new system. For example, Zorach (1972) proposed that the ancestral stock of *Nothonotus* arose west of the Mississippi in the Arkansas or Red River systems and dispersed from there into the Ohio and Tennessee systems, where evolutionary divergence occurred. The Tennessee and Middle Cumberland, and the Green-Barren rivers, seem to have been of great importance as speciation centers. Three dif-

Table 2. Some Land Between the Lakes fishes of Kentucky (from McDonough 1974, and Resh et al. 1972).

Ichthyomyzon bdellium	*Minytrema melanops*
*Lepisosteus oculatus**	*Ictalurus furcatus*
Lepisosteus osseus	*Ictalurus melas*
Lepisosteus platostomus	*Ictalurus natalis*
*Amia calva**	*Ictalurus punctulatus*
Alosa chrysochloris	*Noturus gyrinus*
Hiodon tergisus	*Pylodictis olivaris*
Hybopsis storeriana	*Gambusia affinis*
Nocomis micropogon	*Labidesthes sicculus*
Notropis atherinoides	*Aphredoderus sayanus*
Notropis blennius	*Pomoxis annularis*
Notropis buchanani	*Pomoxis nigromaculatus*
Notropis spilopterus	*Lepomis gulosus*
Notropis whipplei	*Lepomis humilis*
*Opsopoedus emiliae**	*Stizostedion canadense*
Carpiodes carpio	*Stizostedion vitreum*
Carpiodes cyprinus	*Etheostoma asprigene**
Carpiodes velifer	*Etheostoma caeruleum*
Ictiobus bubalus	*Cottus carolinae*
Ictiobus cyprinellus	*Aplodinotus grunniens*
Ictiobus niger	

*Widespread in the Lower Green River portions of the Interior Low Plateau

Table 3. A partial list of fishes from Reelfoot Lake, Tennessee (from Lee et al. 1980, and Parker 1939). Asterisk (*) denotes absence from Low Plateau streams.

Lepisosteus platostomus	*Fundulus notti**
Amia calva	*Fundulus olivaceus*
Alosa alabamae	*Menidia beryllina (audens)**
Hiodon tergisus	*Elassoma zonatum*
Hybognathus nuchalis	*Centrarchus macropterus*
Opsopoedus emiliae	*Lepomis humilis*
Rhinichthys atratulus	*Lepomis symmetricus**
Erimyzon oblongus	*Etheostoma fusiformis**
Noturus gyrinus	*Etheostoma gracilis*
*Umbra limi**	*Etheostoma proeliare*
*Fundulus chrysotus**	

ferent subgenera of darters — four if we accept *Nanostoma* (Page and Burr) — (Table 6), perhaps resulting from various impulses or cycles of invasion from extra-limital stream basins, have markedly diversified within these river systems, doubtless abetted by the notable niche and habitat variability from stream to stream and within drainages.

Actually, the Low Plateau endemic species of the percid subgenera *Nothonotus*, *Catonotus* and *Ulocentra* (including *Nanostoma*) and their nearly 30 species, pose a biogeographic and evolutionary problem of considerable importance that has been inadequately studied. These three groups, in my estimation, are species swarms that have developed in response to mechanisms similar to those proposed by Pflieger (1971) to account for stepwise fish dispersal through the Mississippi and Ohio rivers: "Aggradation subsequent to the last glacial stage produced the environmental conditions now prevailing in the Embayment, restricting further dispersal by upland fishes. All the glacial and interglacial periods were accompanied by alternate entrenchment and aggradation in the Mississippi Embayment, and this would seem to provide an adequate mechanism for the alternate dispersal and isolation of populations east and west of the Embayment."

Thus, this mechanism may have been accompanied by cycles of isolation, adaptation, and speciation, aided by extralimital stream captures that brought congeners back into contact to heighten competition and perhaps establish new patterns of variation and divergence. Whatever the mechanisms and processes, the species swarms are real and the whole problem is deserving of detailed analysis.

Another group of fishes of considerable interest and importance is the ictalurid genus *Noturus*. The fact that most species of *Noturus* avoid cold water (Taylor 1969) indicates a southern origin for the group. The center of greatest abundance of species encompasses Kentucky and Tennessee to Virginia and North Carolina, with a derivative secondary speciation center in the Ozarks of Arkansas and Missouri. Tennessee has the largest number of species, mostly associated with the Tennessee River basin, Kentucky is second followed by Alabama, and the number decreases peripherally. *Noturus gyrinus* (Mitchill), a distinctive lowland species that is widespread and common in the Lower Green and Tradewater systems, gets into Low Plateau streams in western Kentucky and adjacent Indiana and Illinois (Wabash drainage). *Noturus exilis* Nelson is absent from southern Indiana and most of Kentucky, but occurs in extreme southwestern Illinois, much of the Low Plateau of central Tennessee and northern Alabama, and peripheral areas to the north (postglacial) and trans-Mississippian in Oklahoma, Kansas, Missouri, and Arkansas. In the Low Plateau, *Noturus nocturnus* Jordan and Gilbert occurs in the Tennessee River drainage of western Tennessee, northern

Table 4. Wabash River fishes in Indiana derived from Mississippi Embayment and Low Plateau sources (from Gerking 1945, and Blatchley 1938).

Polyodon spathula	*Gambusia affinis*
Lepisosteus oculatus	*Morone mississippiensis*
Lepisosteus spatula	*Centrarchus macropterus*
Alosa chrysochloris	*Lepomis humilis*
Hiodon alosoides	*Ammocrypta clara*
Clinostomus elongatus	*Etheostoma asprigene*
Hybopsis aestivalis	*Etheostoma chlorosomum*
Hybopsis storeriana	*Etheostoma gracile*
Hybognathus hayi	*Etheostoma histrio*
Hybognathus nuchalis	*Etheostoma squamiceps*
Notropis buchanani	*Etheostoma variatum*
Carpiodes carpio	*Percina copelandi*
Carpiodes velifer	*Percina evides*
Cycleptus elongatus	*Percina ouachitae*
Moxostoma carinatum	*Percina sciera*
Moxostoma macrolepidotum	*Percina shumardi*
Noturus nocturnus	

Table 5. Fishes of the Low Plateau derived from lowland and lower Mississippi sources (from Etnier, unpublished).

Notropis buchanani	*Etheostoma chlorosomum*
Notropis maculatus[1]	*Etheostoma gracile*
Notropis shumardi	*Etheostoma histrio*
Notropis venustus	*Etheostoma parvipinne*
Opsopoedus emiliae	*Etheostoma spectabile*[3]
Phenacobius mirabilis[2]	*Etheostoma swaini*
Erimyzon succetta	*Percina evides*[2]
Moxostoma poecilurum[1]	*Percina phoxocephala*
Noturus phaeus[1]	*Percina sciera*
Noturus stigmosus	*Percina shumardi*
Etheostoma asprigene	

[1]Not in Low Plateau
[2]Plains origin
[3]Trans-Mississippian origin

Alabama, and Western Kentucky, from whence it has been able to extend its range up the Ohio into the Wabash River drainage of Illinois and Indiana, the Green River of Kentucky, and old Teays tributaries (Kentucky and Big Sandy rivers) in eastern Kentucky. *Noturus phaeus* Taylor and *N. hildebrandi* (Bailey and Taylor) have ranges that only impinge upon the Low Plateau in Mississippi River drainages of northern Alabama and western Tennessee, *N. phaeus* barely getting into southwestern Kentucky (Terrapin Creek) (Taylor 1979). *Noturus flavus*, being more tolerant of cold water, is distributed throughout much of the upper two-thirds of the Mississippi drainage, including most of the Low Plateau. *Noturus elegans* Taylor, autochthonous to the Barren-Green system of Kentucky and adjacent Tennessee, has an apparently disjunct population in the Tennessee River basin (Duck River). In the Low Plateau, *N. eleutherus* occurs in the Tennessee (no published records from Kentucky stretches of that stream), the Green River, and the Wabash system of Illinois and Indiana. *Noturus stigmosus*, a member of the *furiosus* species complex, avoids most of the Low Plateau but has penetrated into the Green and Salt river drainages of Kentucky and into the Wabash River of Illinois-Indiana. *Noturus miurus* has the widest distribution of all Low Plateau madtoms, having been reported from all drainages.

It seems likely that the ancestral stock of *Noturus* arose somewhere in the lowlands of the Mississippi River basin from a bullhead-like ancestor (Taylor 1969), and spread from there into other parts of America. Using the Tennessee River basin as a speciation center, additional species diverged and spread widely throughout the system in pre- and postglacial times, particularly after development of the Upper Ohio system. Such conclusions are supported by the paucity of *Noturus* species in the Eastern Seaboard drainages.

The occurrence of *Moxostoma* (*Thoburnia*) *atrippine* Bailey — a close relative of the torrent suckers of Virginia — in the Barren River system of the Low Plateau either represents a relict or a case of immigration, extinction in intervening areas, and survival and divergence. The wide hiatus in ranges between population centers in the subgenus *Thoburnia* suggest the latter.

CONCLUSIONS

The examples of Interior Low Plateau aquatic biota discussed here merely represent the complexity of the mechanics and biologistics of understanding such a fauna and flora. I have not discussed other taxa, such as the swarms of unionid pelecypods and decapod crustaceans, because that would have lengthened the paper considerably. However, the distributional patterns of these interesting organisms also very graphically reflect similar conclusions.

Table 6. Endemic fish species of various streams of the Interior Low Plateau and vicinity.

Species	River System	Literature Source
Nothonotus		
Etheostoma bellum	Green	Zorach 1968
Etheostoma chlorobranchium	Tennessee	Zorach 1972
Etheostoma microlepidum	Lower Cumberland	Raney and Zorach 1967
Etheostoma aquali	Duck, Buffalo	Williams and Etnier 1978
Catonotus		
Etheostoma virgatum	Cumberland	Kuehne and Small 1971
Etheostoma obeyense	Upper Cumberland	Kuehne and Small 1971
Etheostoma barbouri	Barren and Green	Kuehne and Small 1971
Etheostoma luteovinctum	Duck and Cumberland	Lee et al. 1980
Etheostoma smithi	Lower Cumberland, Tennessee	Page and Braasch 1976
Etheostoma striatulum	Duck	Page and Braasch 1977
Etheostoma oilvaceum	Caney Fork	Braasch and Page 1979
Etheostoma neopterum	Tennessee	Howell and Dingerkus 1978
Etheostoma species	Tennessee	Howell and Dingerkus 1978
Etheostoma species	Tennessee	Howell and Dingerkus 1978
Etheostoma obeyense	Cumberland	Clay 1975
Ulocentra		
Etheostoma etnieri	Caney Fork	Lee et al. 1980
Etheostoma barrenense	Barren	Page and Burr 1982
Etheostoma rafinesquei	Upper Green, Lower Barren	Page and Burr 1982
Etheostoma simoterum[1]	Tennessee	Lee et al. 1980
Etheostoma atripinne[1]		
Etheostoma species	Obion and Forked Deer	Lee et al. 1980
Etheostoma coosae	Conasauga	Lee et al. 1980
Etheostoma species	Middle Tennessee	Lee et al. 1980
Etheostoma species	Conasauga	Etnier, unpublished
Etheostoma duryi	Tennessee	Lee et al. 1980
Etheostoma species	Lower Green	Burr 1980
Etheostoma species	Blood, Clarks	Burr 1980
Allohistium		
Etheostoma cinereum[2]	Tennessee, Cumberland	Lee et al. 1980
Oligocephalus		
Etheostoma boschungi	Tennessee	Wall and Williams 1974
Catostomidae		
Moxostoma atripinne	Green and Barren	Kuehne and Small 1971
Cyprinidae		
Nocomis effusus	Cumberland, Green, Lower Tennessee	Lachner and Jenkins 1967

[1]Probably conspecific

[2]Principally a Low Plateau species but known from Ridge and Valley Province

The Interior Low Plateau is a unique province in many ways. The region has been periodically convulsed by tectonic readjustments of the crust that stimulated some reorganization of drainages. It was also influenced by the formation and maintenance of the Mississippi Embayment and the isthmus of stable land at the northwest corner of the Low Plateau, and/or by eustatic adjustments of the Embayment, and by stream evolution and modification in extralimital areas, mostly taking the form of headwater piracies between various streams. Pleistocene glaciation caused enormous changes by obliterating much of the old Teays River system and other streams in the unglaciated area, and by successively turning streams westward to form the Upper Ohio River, connecting streams that had never before been in direct contact. This, and the placement of the Mississippi Embayment, conspired to form one of the most unusual hydrologic phenomena in North America. More large rivers find confluence near the junction of Illinois, Indiana, Missouri, and Kentucky than at any other area of equal size in North America: the Ohio, Mississippi, Tennessee, Cumberland, Green, and Wabash rivers. Some of these streams run in nearly ancestral basins, but others do not. The biological function of all these changes was, of course, to open up faunal exchange pathways that had not previously been available. The influence of the Mississippi-Ohio connection upon the repopulation of Indiana and Illinois segments of the Wabash drainage has been very great. During meltback, many small streams were doubtless exterminated and larger ones modified by outwash and deposition, judging from the thickness of known deposits in Indiana and adjacent Kentucky and the fossils contained therein.

Stream-margin and tributary migration ("hopping"), both upstream and downstream, is still a viable hypothesis to explain some observed distributional patterns in small-stream (third order and smaller) species. The meltback of even enormous glaciers is not a constant phenomenon, but one that varies according to season and even time of day, creating impulses of high- and slack-water conditions. Where warmer water flows into glacial streams, the warm water does not mix immediately with the cold. Instead, as I have observed at the Athabascan Ice Field in Canada and at many smaller valley glaciers in British Columbia, Washington, and Oregon, the warmer water flows along the margins of the current. Thus, in the case of Interior Low Plateau drainages, various species of fishes could have found their way into tributaries where they had not previously occurred.

There were, of course, fishes already present in Low Plateau streams prior to the onset of these influences; some of those remain as relicts, either as endemics or as segments of the fauna that are identical with or closely related to segments elsewhere with varying hiatuses intervening. Newly arrived forms from elsewhere may have, because of

narrow habitat or niche requirements, remained close to the points of entry (as in the case of some of the headwater species), or they may have spread inexorably through systems, progressively coming into competition with members of the preexisting fauna. Such competition may have caused some minor extinctions here and there by way of niche replacement, but it probably stimulated subdivision of niches and, apparently, considerable sequences of divergence, speciation, and other types of faunal readjustments. Some speciation may have been stimulated by the presence of unoccupied niches, by the habitat fluctuations associated with long-term geologic influences, and by differences between various segments of Low Plateau drainages.

All these influences have acted in concert to create a superior aquatic fauna in the streams and rivers of the Interior Low Plateau, but one which has remained relatively poorly understood until recent times, particularly in its relationships to extralimital drainages. Now a new factor has been superimposed upon natural ones, a factor that not only threatens the integrity of the fauna and flora (Branson 1977), but one that also threatens our ability to understand this biota. The results of preimpoundment studies indicate that some species, present prior to damming of streams, are now either very rare or unknown from afflicted areas. An example is *Hybognathus nuchalis* (pers. comm., David Etnier and students, following study of University of Michigan holdings). Every major stream that flows through the Low Plateau bears dams, sometimes multiple ones. These structures have vastly modified habitats, upset temperature regimens, and diminished nutrient flow through the systems. Exotic species and transplanted ones, such as striped bass, trout, and threadfin shad, have gotten into the system, creating stress that was not earlier present. Previously autonomous drainages are now interconnected. For example, a navigation canal joins the Cumberland and Tennessee rivers at Land Between the Lakes; other connections are planned, such as the Tennessee-Tombigbee Waterway. Coal mining and channelization continue to inflict adverse changes in many Low Plateau streams. Other recent influences are steadfastly afflicting this unique fauna, bringing many species to levels of concern (Branson et al. 1981). Most are associated with human population pressures, the changing financial picture, and the energy crisis. Hopefully, we have learned enough to preserve at least the principal genomes of the Low Plateau biota.

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NEW MANAGING EDITOR

Alexa C. Williams, Managing Editor of *Brimleyana* since its inception early in 1979, has resigned her position as Director of Publications and Public Relations at the museum. She will be Associate Editor of a new international physiology journal edited by Knut Schmidt-Nielsen at Duke University, Durham. We wish Alexa all the best in this challenging endeavor. Alexa's replacement, and new Managing Editor of *Brimleyana*, is Eloise F. Potter. As an author, reviewer, and longtime Editor of *The Chat*, quarterly bulletin of the Carolina Bird Club, Inc., Eloise is conversant with all aspects of journal production and is a welcome addition to our staff.

SUBSCRIPTIONS AND EXCHANGES

The editors anticipate two issues of approximately 150 pages each annually, but may not always be able to adhere to this schedule. Subscription rates are for the two forthcoming issues, unless the subscriber indicates otherwise.

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DATE OF MAILING

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ERRATA

Brimleyana No. 10:

Page 3: line 12, insert *lewisi* after *Necturus maculosus*.

Page 32: LITERATURE CITED, between Neill 1963 and Shoop and Gunning 1967 insert:

Nickerson, Max A., and R. E. Ashton, Jr. 1983. Lampreys in the diet of hellbender *Cryptobranchus alleganiensis* (Dundin), and the Neuse River waterdog *Necturus lewisi* (Brimley). Herpetol. Rev. *14*(1):10.

INFORMATION FOR CONTRIBUTORS

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CONTENTS